AN ENERGY BUDGET OF THE ATLANTIC HERRING (CLUPEA HARENGUS HARENGUS)

MICHAEL DOUGLAS McGURK

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AN ENERGY BUDGET OF THE ATLANTIC HERRING (*CLUPEA HARENGUS HARENGUS*)

by

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A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science

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St. John's Newfoundland

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Abstract

The study analyzes the seasonal energy flows within adult Atlantic herring. The seasonal cycles of the condition indices, the lipid and water content and the energy densities of the body and the gonads were measured for a stock complex off the Avalon Peninsula, Newfoundland.

The conditions indices and the energy densities were combined in a simulation model to calculate a seasonal energy budget for herring of ages 3-11+. The model was validated by comparing the seasonal and annual rations rates, the exponent of the fecundity-length equation and the gross growth efficiencies with values reported in the literature.

A sensitivity analysis of the model revealed that the model output is most sensitive to variation in the metabolic rate parameters and least sensitive to variations in the data on the conditions indices, the energy densities and the annual growth increments.

The model was used to examine the consequences of three strategies of energy allocation between the soma and the gonads. There is a tradeoff between the fecundity and the body condition index but the exact form of the relationship is unknown and so the optional strategy cannot be identified.

Acknowledgements

I wish to express my sincere thanks to my supervisor Dr. J.M. Green, for criticism and guidance throughout this study.

Thanks and appreciation are also extended to Dr. D. McKone and Dr. G. Winters of the Department of Fisheries and Oceans for helping to initiate this project and for their patient consultation, to Mr. K. Spencer and the technicians of the Fish Inspection Laboratory for their generous assistance in the chemical analysis of the samples, and to Mr. R. Chaulk and Mr. R. Sullivan of the Department of Fisheries and Oceans for assistance in locating the samples and for ageing the fish. I gratefully acknowledge financial support in the form of a University Fellowship and a subvention grant from the Department of Fisheries and Oceans to Dr. J.M. Green.

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Introduction

Energy budget models have been published for a number of fish species: the Pacific sardine, Sardinops caerulea (Lasker 1970), the plaice Pleuronectes platessa, (Steele and Edwards 1970), the American plaice Hippoglossoides platessoides (MacKinnon 1973), the yellowfin tuna Thunnus albacares (Sharp and Francis 1976), and the yellow perch Perca flavescens, and the walleye Stizostedion vitreum vitreum (Kitchell et al. 1977). Two workers who presented complete energy budgets supported by data are MacKinnon (1973) and Lasker (1970). On the whole, however, the distribution and expenditure of energy in fishes in not well understood.

The aforementioned models can consist of two parts: a model of the energetics of an individual fish and, in some, a population dynamics model. If the two are combined an estimate of the energy flow pattern and of the magnitude of the flows is obtained. One aim of these studies is the estimation of the seasonal and annual rates of food consumption. Comparison of these rates with the rates of food production are then made in order to determine if food limitation is present or absent. Another objective is the simulation of growth rates under varying regimes of temperature and food availability. Additional areas of interest include the ecological efficiencies of the population and the age distribution of the rates of food consumption and metabolism. Almost all of the models have been concerned

exclusively with juvenile and adult fish. An exception is that of Laurence (1977) who modelled the energy requirements of the larvae of the winter flounder, Pseudopleuronectes americanus, in an attempt to determine the critical plankton densities below which the larvae starved. Energetics models have also been constructed to estimate the rate of uptake of pollutants by fish; Norstrom et al. (1976) described an energetics-based predictive model of PCB (polychlorinated biphenyls) and methylmercury accumulation in yellow perch. Finally, Ware (1975, 1978) has utilized energetics principles in an analysis of the optimum swimming speed of pelagic fish.

The general objective of this study is the analysis of the seasonal energy flows within individual adult Atlantic herring. There are two parts of this report. The first part describes the seasonal cycle of the condition indices of the body and the gonads and the seasonal cycle of the lipid and water composition and of the energy densities of the soma and the gonads. The second part describes a model which integrates the energy density data with data on the condition indices to calculate the magnitude of the seasonal energy flows within the fish. The model is then used to calculate an index of fitness for each of three strategies of energy allocation between the soma and the gonads.

PART I

Materials and Methods

Sampling

Ten samples of herring were obtained from commercial catches between March 1, 1977 and February 6, 1978. Samples were taken every six to eight weeks except during the pre-spawning and spawning period when they were taken every two to three weeks.

The seasonal nature of the inshore herring fishery made it impossible to obtain all samples from one population. Eight of the ten samples were taken from the Placentia Bay-St. Mary's Bay management unit, one was taken from the adjacent Conception Bay-Southern Shore management unit and one from the Bonavista Bay management unit (Fig. 1). It is assumed that the energy cycles of these three units are synchronous. This is reasonable since the mean date of spawning for the spring-spawners in each unit are within a week of each other (G. Winters, personal communication). Also, recent tagging studies (G. Winters, personal communication) have shown that migration occurs between the first two units but because the extent of intermixing is unknown they are separated for management purposes.

A sample consisted of 50-60 specimens taken from the catch of a commercial vessel. The catch was sampled either on board the ship or in the fish processing plant several hours after off-loading. The fish were packed in ice and transported to the laboratory. There 10-15 fish

Fig. 1. Map showing the east coast of Newfoundland and the locations of the samples. Each dot is one sample.


BONAVISTA
BAY
CONCEPTION
BAY
SOUTHERN
SHORE
PLACENTIA
BAY
ST. MARY'S
BAY

of each sex were chosen and length, defined as the distance from the tip of the snout to the end of the longest caudal ray, was measured to 0.1 cm. Wet body weight was measured to 0.1 g. The otoliths were removed for age determination. The weight of the stomach contents, if any, was taken to 0.1 g and was later used to correct the wet body weight. The gonads were weighed to 0.1 g, sexed and assigned a maturation stage (Anonymous 1964). The body was separated into three compartments: the head, the gonads and the soma. The head was treated as a separate entity because it is assumed to play a negligible role in the internal energy flows of the body due to its lack of energy storage organs.

A subsample of gonad tissue was placed in a plastic bag which was immediately sealed and frozen at -20 C for later lipid and water analysis. The remainder of the gonad was reserved for calorimetry. The head and the vertebral column, including the caudal fin, were removed and weighed to 0.1 g. The filets and the viscera, hereafter referred to as the soma, were combined and minced in a meat grinder and then homogenized in a heavy-duty Waring blender. A subsample of the homogenate was placed in a plastic bag which was immediately sealed and frozen at -20 C for later lipid and water analysis. Another subsample was reserved for calorimetry.

Twice during the year a number of heads were ground, homogenized and subsampled for lipid and water analysis and for calorimetry.

Water

The frozen subsamples were thawed, then transferred to tared aluminum pans, weighed and dried in an oven at 100 C for two days. The pans were cooled in a dessicator and then weighed again. Mean percent water was computed from duplicate samples and never differed by more than 1%.

Lipid

Percent lipid was determined by the Soxhlet method (Association of Official Analytical Chemists 1975) using ether as a solvent. Mean percent lipid was computed from duplicate samples of dried tissue. A third replicate was performed if the difference between the duplicates was greater than 1% and the mean percent lipid was then computed using the two values which differed by less than 1%.

Calorimetry

The fresh subsamples of gonad and soma were dried in an oven at 100 C for two days and then ground to a fine powder using either a mortar and pestle or a ball mill grinder. All subsamples were stored in a dessicator until bombed. Ten subsamples of soma and ten subsamples of gonad of each sex were bombed in duplicate with a Parr adiabatic calorimeter. All energy values were corrected for the heat of fuse wire combustion and for the heat of acid formation. An additional test was performed if the first two tests differed by more than 126 joules $\cdot g^{-1}$. All tests were done within 30 days of procuring a sample in order to avoid possible inaccuracies due to tissue oxidation.

Results

Condition Indices

The sample number, date, location and the number of specimens processed of each sample are listed in Table I. The measurements of length and weight of each specimen are listed in Appendix A.

The mean body condition index, C, is defined as

(1) $$C = W \times 10^6/L^3,$$

where W is body weight in grams and L is the length in millimeters. The mean C of each sex of each sample is shown in Table II. T-tests revealed that, except for the sample taken on October 25, there are no significant differences between the mean C's of the two sexes. The means of the sexes were combined and are shown in Fig. 2A. There is a decrease in mean C over the winter and spring followed by an increase over the summer months to a peak in December. The sudden drop in mean C at the time of spawning was calculated by subtracting the mean gonad weight at spawning from the mean body weight at spawning. The post-spawning mean C was calculated as 6.60 for a wide range of body weights. The dotted line was drawn by eye.

The mean monthly gonad condition index I, defined as

(2) $$I = W_{gonad}/W,$$

is shown in Fig. 2B and 2C. The ovaries appear to increase in condition throughout the winter and spring whereas the

Table I. List of the sample dates and locations.

Sample number	Date	Area	Number of fish measured	Number for lipid and water	Number for calorimetry
1	Mar. 1	Placentia Bay	36	22	0
2	Mar. 31	Placentia Bay	26	24	12
3	Apr. 29	St. Mary's Bay	36	0	14
4	May 18	St. Mary's Bay	28	23	19
5	June 3	St. Mary's Bay	26	23	22
6	Aug. 12	Southern Shore	23	17	17
7	Oct. 25	Bonavista Bay	45	20	20
8	Dec. 20	St. Mary's Bay	24	21	18
9	Jan. 17	Placentia Bay	24	0	0
10	Feb. 6	St. Mary's Bay	24	20	0
		Total	292	170	122

Table II The mean body condition index (± 1 s.d.) of each sex of each sample. The bracketed number is the sample size. NS means there is no significant difference between the means and S means there is a significant difference.

Sample Date	Male	Female	
Mar. 1, 1977	8.88 ± 0.94 (14)	8.69 ± 0.55 (22)	NS
Mar. 31, 1977	8.27 ± 0.62 (12)	8.57 ± 0.46 (13)	NS
April 29, 1977	7.80 ± 0.31 (17)	8.25 ± 0.44 (18)	NS
May 18, 1977	7.67 ± 0.68 (12)	7.92 ± 0.66 (16)	NS
June 3, 1977	7.96 ± 0.39 (12)	7.78 ± 0.74 (13)	NS
Aug. 12, 1977	7.66 ± 0.49 (14)	7.46 ± 0.41 (9)	NS
Oct. 25, 1977	8.23 ± 0.39 (21)	7.69 ± 0.41 (24)	S ($P < 0.01$)
Dec. 20, 1977	8.56 ± 0.68 (12)	8.20 ± 0.37 (12)	NS
Jan. 17, 1978	8.47 ± 0.53 (12)	8.19 ± 0.41 (12)	NS
Feb. 6, 1978	7.80 ± 0.54 (12)	7.73 ± 0.55 (12)	NS

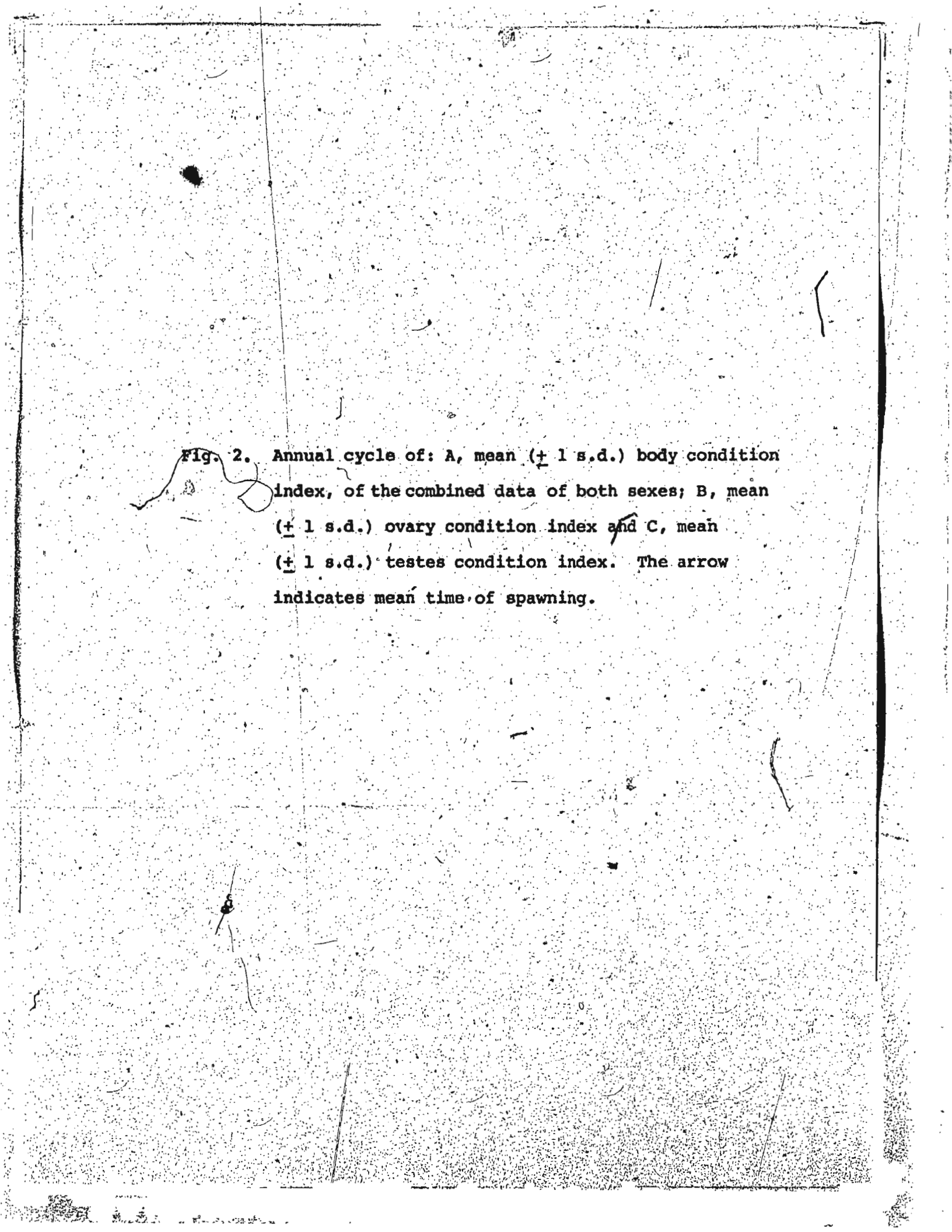
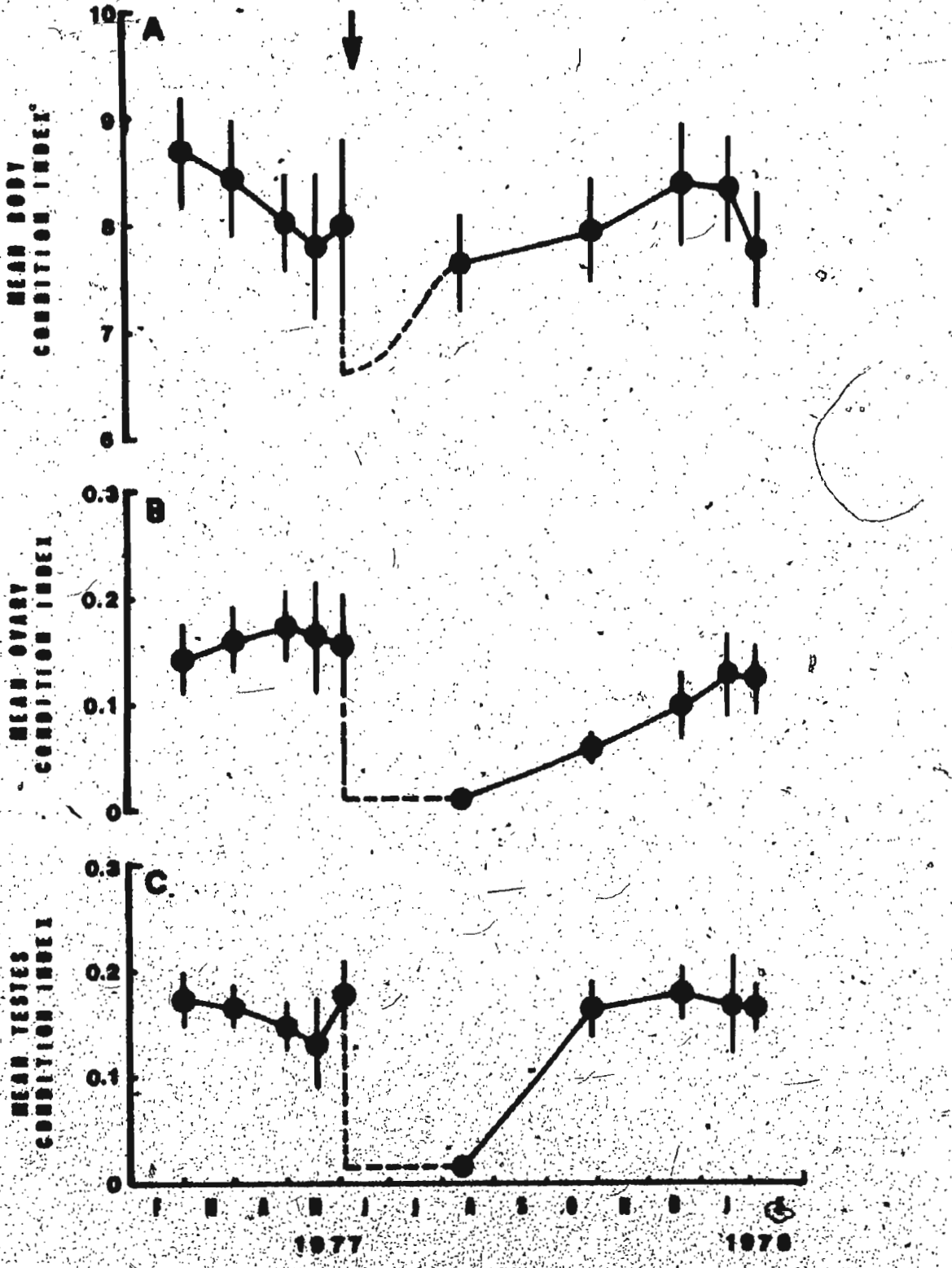


Fig. 2. Annual cycle of: A, mean (± 1 s.d.) body condition index, of the combined data of both sexes; B, mean (± 1 s.d.) ovary condition index and C, mean (± 1 s.d.) testes condition index. The arrow indicates mean time of spawning.


A
B
C
10
9
8
7
6
0.3
0.2
0.1
0
1977
1978

testes appear to remain constant or even to decrease in condition over the same period. The testes grow rapidly over the summer and reach their maximum condition in October. The ovaries grow at a slower rate, reaching their maximum condition immediately before spawning.

In order to determine if there is any variation of condition index with age the mean condition indices of each sample were separated into age classes as is shown in Tables III, IV and V. Immatures were not included in these tables. Examination of the tables shows that there is a possible positive correlation between the condition indices and age. In order to test this an index, D, of the deviation of the monthly means at age from the monthly mean for the entire sample, $\bar{C}$, was first calculated. It is defined as

$$D_i = \left(\sum^{j}(C_{ij} - C_j)n_{ij}\right)/\sum^{j} n_{ij} \tag{3}$$

where n is the sample size of the monthly mean at age, i is age and j is the sample number. The D of the body condition index is significantly correlated with age ($r = 0.83$; $0.01 < P < 0.05$) as is that of the ovaries ($r = 0.97$; $P > 0.01$). The D of the testes is not correlated with age ($r = 0.011$; $P < 0.05$). The scatter of the points is shown in Figs. 3A, 3B and 3C. A regression of D on age was calculated for the body and the ovary respectively.

body:

$$D = 0.0660\ (\text{Age}) - 0.5105;\ R^2 = 0.70 \tag{4a}$$

Table III Mean monthly body condition index for each age. The sample size is enclosed in brackets. Only sexually mature fish are included in the calculation of the mean.

Month	Age 3	4	5	6	7	8	9	10	11+	Mean ± 1s.d.
Feb.	-	-	8.65 (7)	-	8.85 (1)	8.45 (4)	8.48 (10)	-	8.92 (13)	8.68 ± 0.53 (35)
March	-	-	8.13 (7)	8.86 (1)	-	8.27 (4)	8.71 (8)	8.25 (3)	8.64 (3)	8.43 ± 0.54 (26)
April	-	-	-	-	-	7.96 (11)	8.02 (18)	-	8.22 (6)	8.03 ± 0.44 (35)
May	-	-	7.51 (3)	6.73 (1)	7.45 (3)	7.99 (5)	7.83 (9)	8.18 (1)	8.08 (6)	7.81 ± 0.67 (28)
June	-	8.30 (1)	-	-	8.09 (1)	7.90 (11)	7.66 (9)	-	8.14 (3)	7.98 ± 0.83 (25)
July	-	-	-	-	-	-	-	-	-	-
Aug.	-	-	-	-	-	7.59 (4)	7.72 (11)	7.42 (1)	7.38 (7)	7.64 ± 0.45 (23)
Sept.	-	-	-	-	-	-	-	-	-	-
Oct.	-	-	-	-	-	8.57 (3)	7.92 (29)	7.78 (2)	7.86 (11)	7.94 ± 0.48 (45)
Nov.	-	-	-	-	-	-	-	-	-	-

Table III Mean monthly body condition index for each age. The sample size is enclosed in brackets. Only sexually mature fish are included in the calculation of the mean. (Continued)

Month	Age 3	4	5	6	7	8	9	10	11+	Mean ± 1s.d.
Dec.	-	-	8.32 (2)	-	-	-	8.35 (6)	-	8.40 (16)	8.38 ± 0.57 (24)
Jan.	-	8.06 (8)	7.85 (1)	8.45 (6)	-	-	-	-	8.54 (9)	8.33 ± 0.49 (24)
Feb.	-	7.56 (3)	7.32 (4)	7.65 (2)	8.27 (1)	-	-	7.87 (10)	8.05 (4)	7.77 ± 0.53 (24)
D	-	-0.206	-0.234	-0.017	-0.050	-0.015	-0.025	0.017	0.405	

Table IV Mean monthly ovary index for each age. The sample size is enclosed in brackets. Only sexually mature fish are included in calculating the mean.

Month	3	4	5	6	7	8	9	10	11+	Mean ± 1s.d
Feb.	-	-	0.1003 (5)	-	0.1546 (1)	0.0976 (1)	0.1524 (6)	-	0.1640 (9)	0.1429 ± 0.0331 (22)
March	-	-	0.1252 (3)	0.1664 (1)	-	0.1728 (1)	0.1697 (6)	0.1592 (1)	0.2040 (1)	0.1612 ± 0.0303 (13)
April	-	-	-	-	-	0.1491 (5)	0.1790 (10)	-	0.2007 (3)	0.1743 ± 0.0315 (18)
May	-	-	0.1108 (2)	0.0464 (1)	0.1434 (2)	0.1988 (1)	0.2066 (4)	0.2088 (1)	0.1722 (5)	0.1656 ± 0.0504 (16)
June	-	0.0745 (1)	-	-	-	0.1722 (4)	0.1513 (5)	-	0.1755 (2)	0.1559 ± 0.0484 (12)
July	-	-	-	-	-	-	-	-	-	-
Aug.[a]	-	-	-	-	-	0.0136 (3)	0.0123 (4)	0.0145 (1)	0.0150 (1)	0.0133 ± 0.0021 (9)
Sept.	-	-	-	-	-	-	-	-	-	-
Oct.	-	-	-	-	-	-	0.0607 (15)	0.0592 (2)	0.0605 (7)	0.0605 ± 0.0128 (24)
Nov.	-	-	-	-	-	-	-	-	-	-
Dec.	-	-	-	-	-	-	0.1046 (2)	-	0.0979 (10)	0.0990 ± 0.0296 (12)

Table IV Mean monthly ovary index for each age. The sample size is enclosed in brackets. Only sexually mature fish are included in calculating the mean. (Continued)

Month	3	4	5	6	7	8	9	10	11+	Mean ± 1.s.d
Jan.	-	0.0901 (2)	0.0886 (1)	0.1291 (4)	-	-	-	-	0.1498 (5)	0.1279 ± 0.0391 (12)
Feb.	-	0.0623 (1)	0.1113 (3)	-	0.1072 (1)	-	-	0.1378 (4)	0.1453 (3)	0.1238 ± 0.0310 (12)
D		-0.0546	-0.0362	-0.0208	-0.0136	-0.0073	0.0059	0.0106	0.0119	

a. Probably sexed incorrectly and so represents mean value for both sexes

Table V. Mean monthly testes index for each age. The sample size is enclosed in brackets. Only sexually mature fish are included in the calculation of the mean.

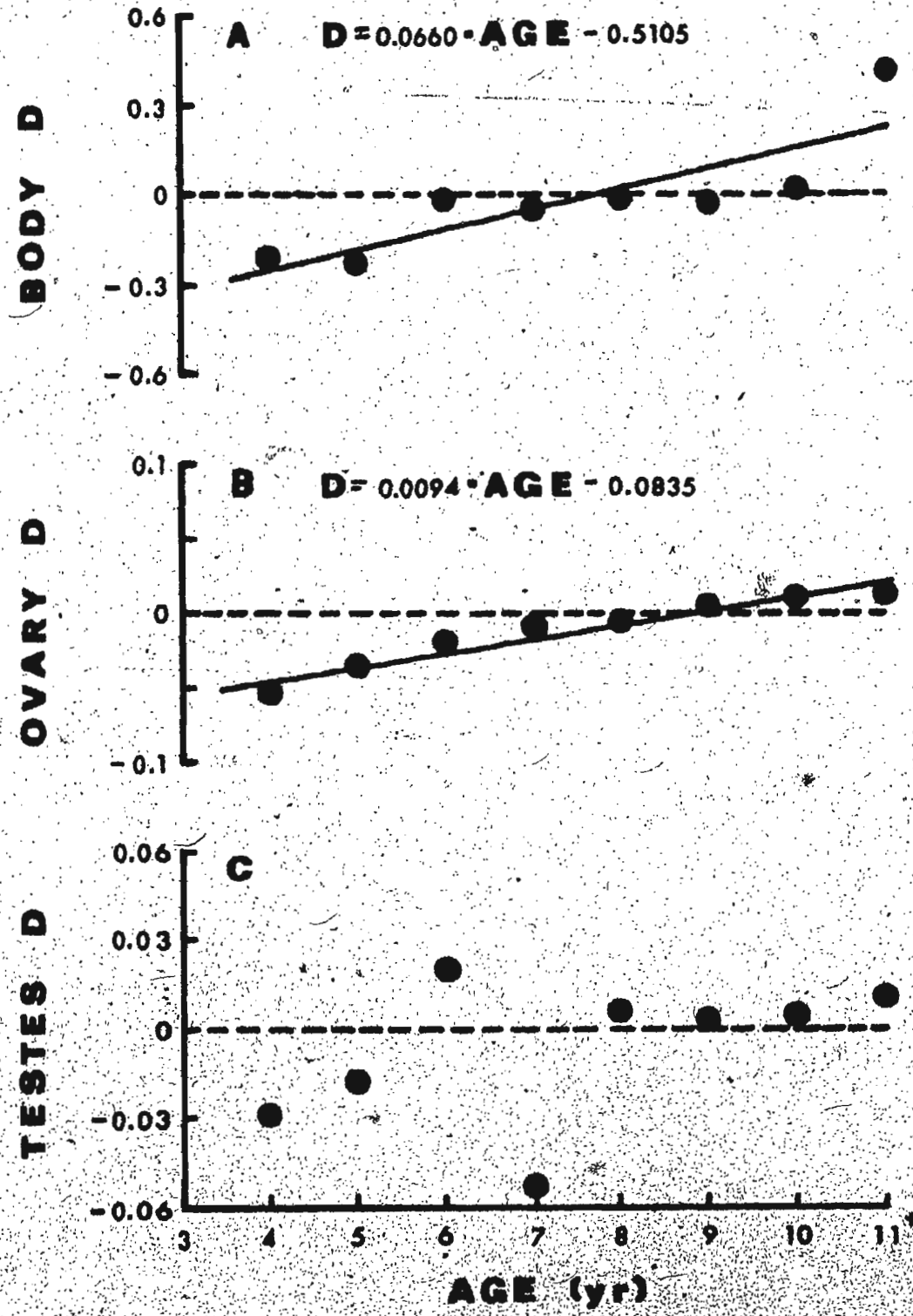
Month	3	4	5	6	7	8	9	10	11+	Mean ± 1s.d.
Feb.	-	-	0.1381 (3)	-	-	0.1711 (2)	0.1778 (4)	-	0.1929 (4)	0.1723 ± 0.0252 (13)
March	-	-	0.1615 (4)	-	-	0.1571 (3)	0.1736 (2)	0.1809 (2)	0.1683 (2)	0.1664 ± 0.0181 (13)
April	-	-	-	-	-	0.1542 (6)	0.1394 (8)	-	0.1553 (3)	0.1474 ± 0.0225 (17)
May	-	-	0.1187 (1)	-	0.0541 (1)	0.1421 (4)	0.1453 (5)	-	0.1092 (1)	0.1314 ± 0.0422 (12)
June	-	-	-	-	0.1486 (1)	0.1806 (6)	0.1927 (4)	-	0.1181 (1)	0.1768 ± 0.0313 (12)
July	-	-	-	-	-	-	-	-	-	-
Aug.	-	-	-	-	-	0.0405 (1)	0.0148 (7)	-	0.0143 (6)	0.0164 ± 0.0079 (14)
Sept.	-	-	-	-	-	-	-	-	-	-
Oct.	-	-	-	-	-	0.1830 (3)	0.1602 (14)	-	0.1694 (4)	0.1640 ± 0.0270 (21)
Nov.	-	-	-	-	-	-	-	-	-	-
Dec.	-	-	0.1501 (2)	-	-	-	0.1796 (4)	-	0.1881 (6)	0.1789 ± 0.0245 (12)

Table V. Mean monthly testes index for each age. The sample size is enclosed in brackets. Only sexually mature fish are included in the calculation of the mean. (Continued)

Month	3	4	5	6	7	8	9	10	11+	Mean ± 1.s.d.
Jan.	-	0.1333 (6)	-	0.2067 (2)	-	-	-	-	0.1987 (4)	0.1673 ± 0.0459 (12)
Feb.	-	0.1521 (2)	0.1609 (1)	0.1663 (2)	-	-	-	0.1674 (6)	0.1785 (1)	0.1651 ± 0.0206 (12)
D	-	-0.0288	-0.0179	0.0203	-0.0528	0.0063	0.0031	0.0054	0.0109	

a. Probably sexed incorrectly and so represents a mean value for both sexes.

Fig. 3. The relationship between D and age for: A, the body; B, the ovary and C, the testes.


A
D = 0.0660 • AGE - 0.5105
BODY D
0.6
0.3
0
-0.3
-0.6
B
D = 0.0094 • AGE - 0.0835
OVARY D
0.1
0
-0.1
C
TESTES D
0.06
0.03
0
-0.03
-0.06
3
4
5
6
7
8
9
10
11
AGE (yr)

ovary:

(4b) $D = 0.0094\ (Age) - 0.0835;\ R^2 = 0.95$

Lipid and Water

The precent lipid and percent water of each compartment, based on the wet weight of the compartment, of each specimen analyzed are listed in Appendix B. T-tests revealed that there were no significant differences ($P > 0.05$) between the percentages of lipid and water of the soma of the males and that of the females at any time of the year. The two sets of data were therefore pooled. The annual cycles of mean ($\pm$ 1 s.d.) percent water and mean ($\pm$ 1 s.d.) percent lipid of the soma, the ovaries and the testes are shown in Figs. 4 and 5. The gonads of the specimens of the August 12 sample were sexed incorrectly and were therefore omitted. The percent water of all these compartments increased over the winter and spring to a maximum immediately before spawning. The precent water of the soma was at a minimum in mid-summer and gradually increased over the fall and early winter, whereas the percent water of both the ovary and the testes steadily decreased from a peak in October. The percent lipid of the soma, ovary and testes followed a pattern that is essentially the opposite of that of the percent water.

In order to determine if the percent lipid of the soma varies with body length the data on percent lipid of each sample was grouped into length classes and a mean value for each length class calculated as is shown in Table

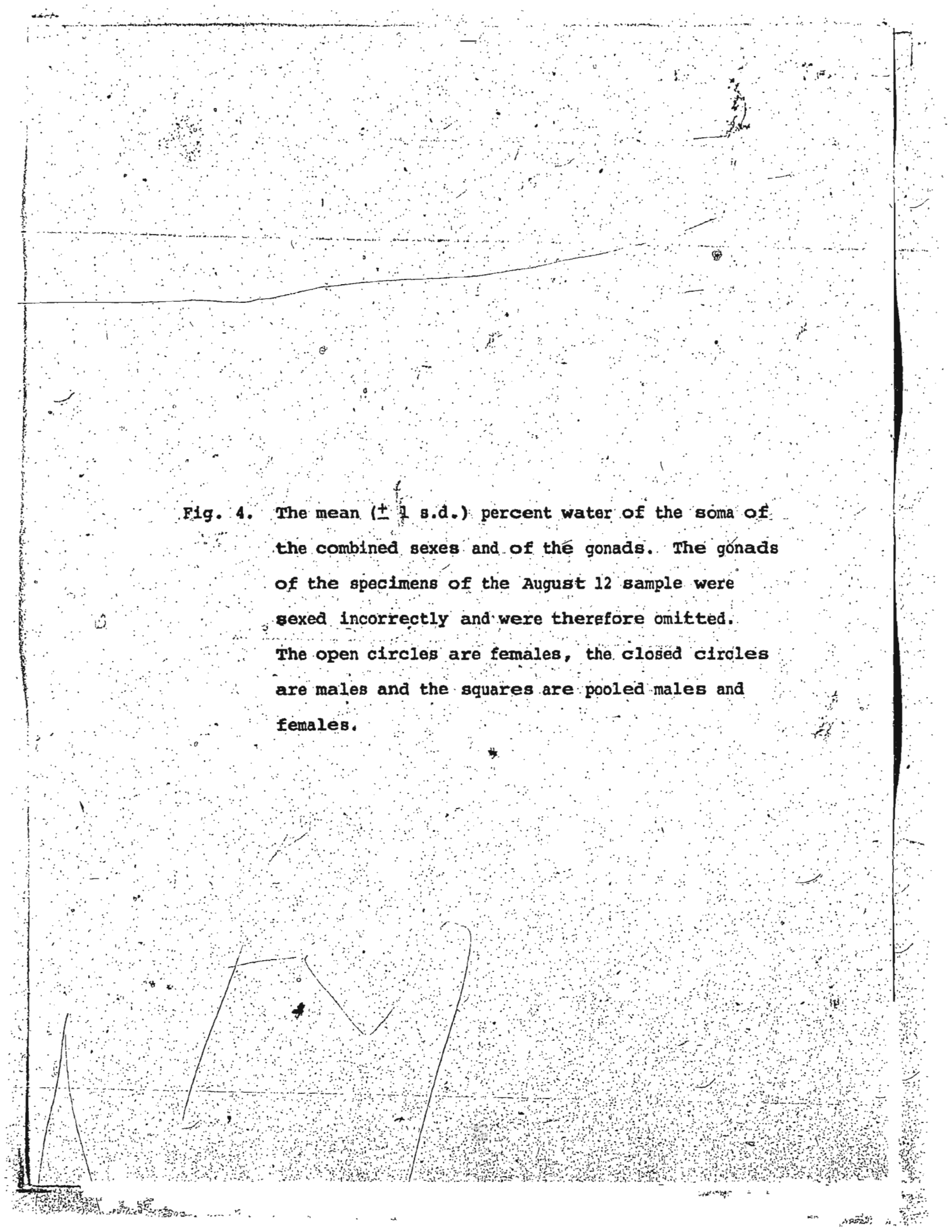
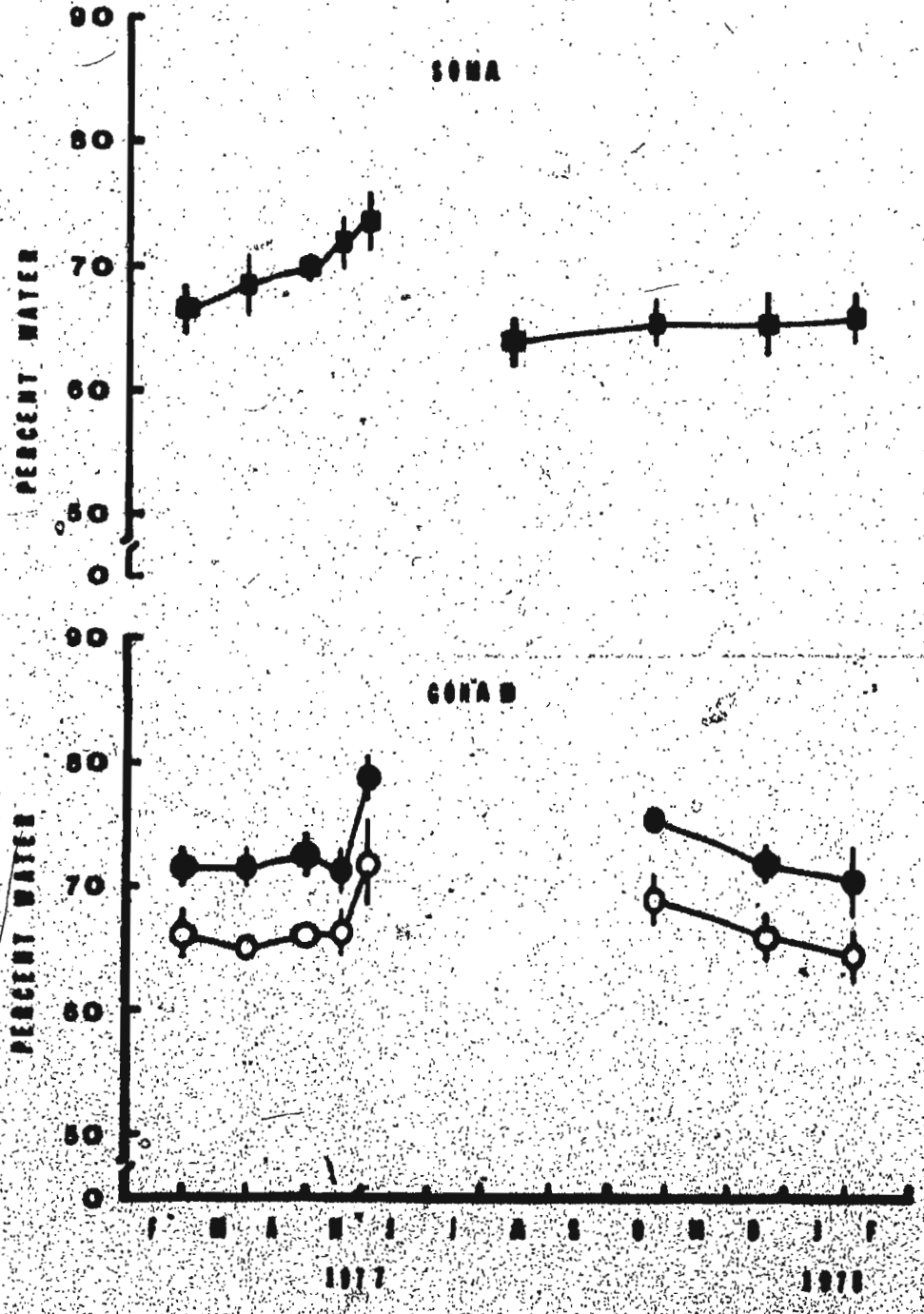


Fig. 4. The mean (± 1 s.d.) percent water of the soma of the combined sexes and of the gonads. The gonads of the specimens of the August 12 sample were sexed incorrectly and were therefore omitted. The open circles are females, the closed circles are males and the squares are pooled males and females.


90
80
70
60
50
0
PERCENT WATER
SOMA
90
80
70
60
50
0
PERCENT WATER
SOMA B
F M A M J J A S O N D J F
1977
1978

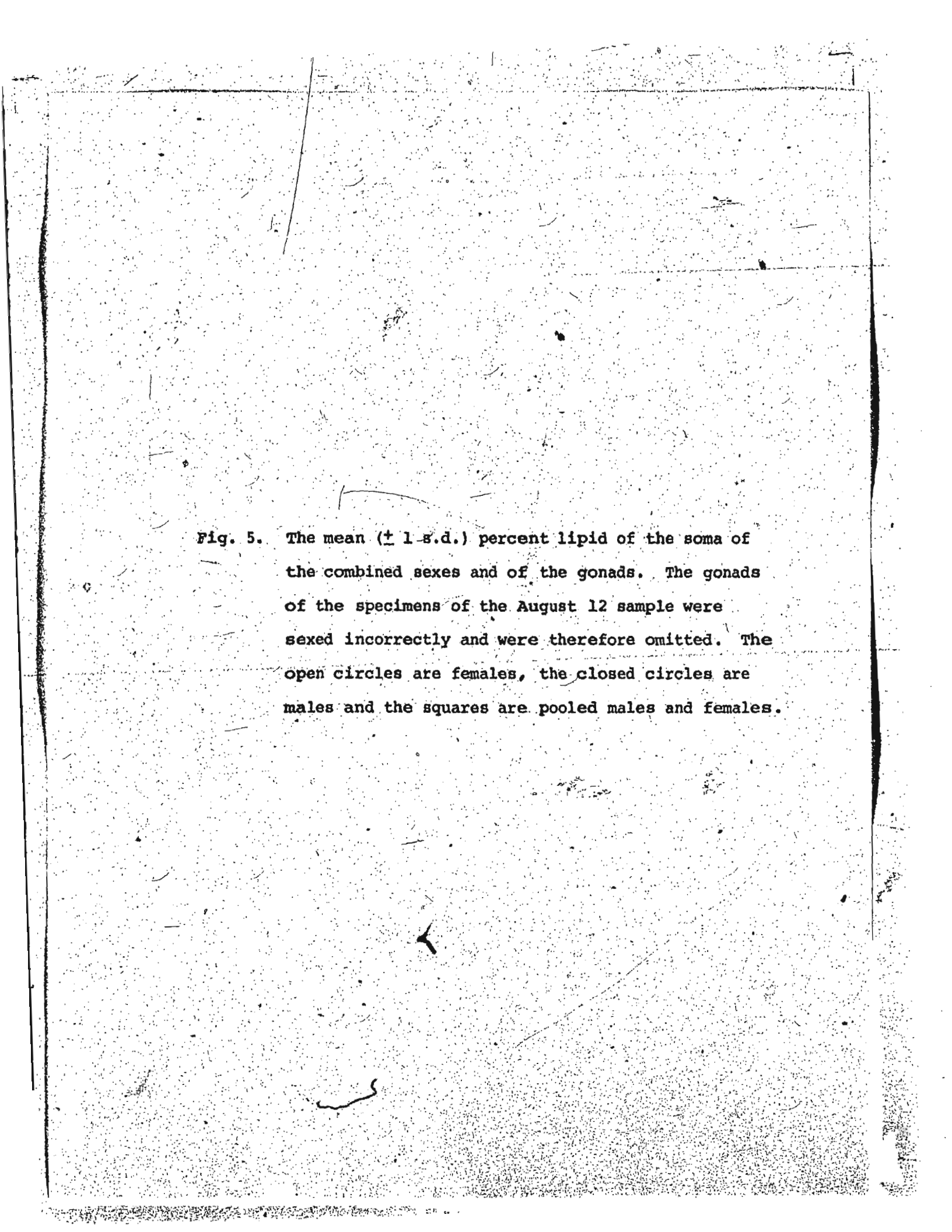
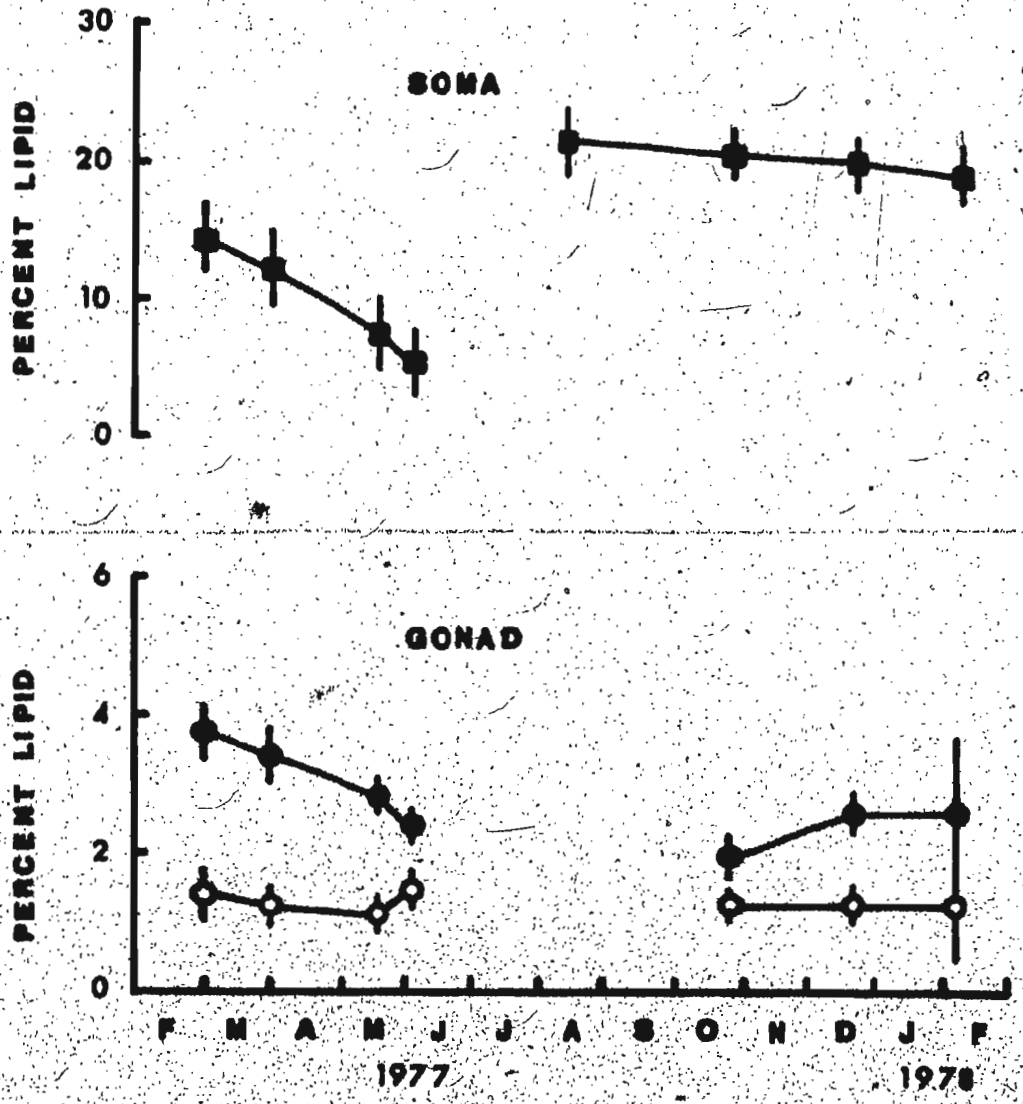


Fig. 5. The mean (± 1 s.d.) percent lipid of the soma of the combined sexes and of the gonads. The gonads of the specimens of the August 12 sample were sexed incorrectly and were therefore omitted. The open circles are females, the closed circles are males and the squares are pooled males and females.


SOMA
PERCENT LIPID
30
20
10
0
GONAD
PERCENT LIPID
6
4
2
0
F M A M J J A S O N D J F
1977
1978

VI. Examination of Table VI shows that there is no apparent trend of percent lipid of the soma with length.

Examination of the percent lipid and percent water of the compartments of individual specimens suggests that lipid and water make up a constant percent of the wet weight of a compartment. The mean (± 1 s.d.) combined percent is $80.21 \pm 0.99\%$ for the soma, $75.89 \pm 2.84\%$ for the testes and $68.10 \pm 3.29\%$ for the ovaries. Correlation analysis revealed that the percent lipid of the soma is highly negatively correlated with the percent water ($r = -0.98$; $P < 0.01$), as are the percent lipid and percent water of the testes ($r = -0.70$; $P < 0.01$). The percent lipid of the ovaries, however, is not significantly correlated with the percent water ($r = 0.24$; $P > 0.05$). This means that it is possible to use percent water as a prediction of percent lipid for the soma and the testes. The ovaries have a mean (± 1 s.d.) percent lipid of $1.23 \pm 0.33\%$ at all times of the year. Percent lipid was linearly regressed on percent water for the soma and the testes and the following equations were obtained (Fig. 6).

soma:

(5a) $\%\ \text{lipid} = 86.71 - 1.095\ (\%\ \text{water})$,

Testes:

(5b) $\%\ \text{lipid} = 13.81 - 0.150\ (\%\ \text{water})$.

Energy Density

The energy densities ($kj \cdot g^{-1}$ wet weight) of each compartment of each specimen are listed in Appendix C.

Table VI The mean percent lipid of the soma of the combined sexes separated into length classes for each sample. The number of specimens is in parentheses.

Sample Number	29.1-30.0	30.1-31.0	31.1-32.0	32.1-33.0	33.1-34.0	34.1-35.0	35.1-36.0	36.1-37.0	37.1-38.0
1	-	-	-	-	-	-	-	-	-
2	-	-	-	16.94 (2)	13.88 (6)	15.14 (8)	12.50 (5)	16.41 (1)	-
3	-	-	-	13.00 (4)	12.36 (9)	10.96 (7)	13.57 (2)	14.18 (1)	-
4	-	-	-	-	-	-	-	-	-
5	-	-	8.26 (3)	5.66 (5)	5.61 (4)	8.05 (6)	9.41 (3)	7.43 (2)	-
6	7.48 (1)	-	3.70 (1)	6.22 (5)	5.20 (8)	5.39 (5)	6.17 (3)	-	-
7	-	-	-	-	16.66 (8)	16.03 (3)	16.67 (5)	16.58 (1)	-
8	-	-	-	15.27 (2)	14.88 (11)	16.02 (3)	16.13 (3)	17.00 (1)	-
9	-	-	-	15.88 (1)	15.94 (2)	14.32 (6)	14.65 (8)	15.36 (4)	-
10	-	-	-	-	-	-	-	-	-
11	-	16.34 (1)	13.45 (1)	14.65 (2)	15.00 (5)	13.98 (4)	12.89 (3)	10.76 (3)	17.22 (1)

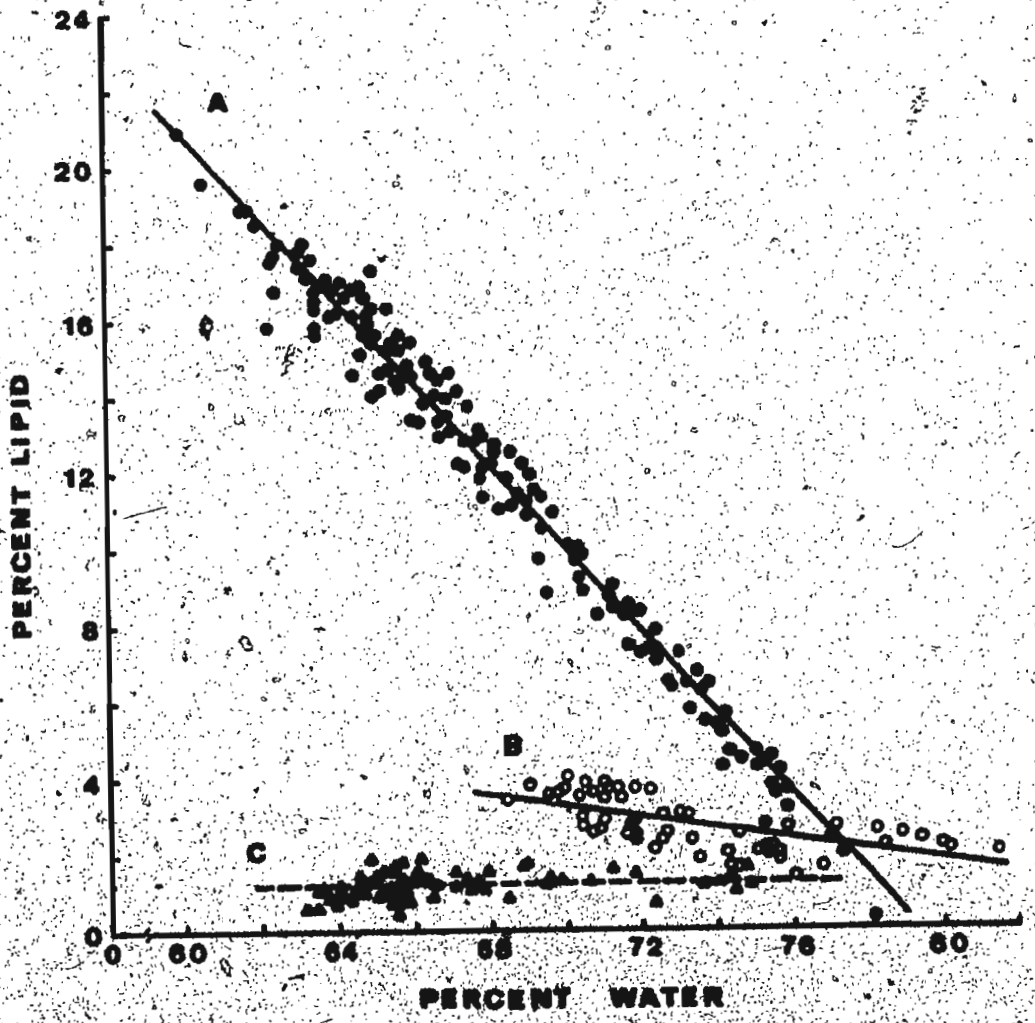
Fig. 6. The relationship between the percent lipid and the percent water of: A, the soma of the combined sexes; B, the testes and C, the ovaries. The regression equation for A is:

% lipid = 86.710 - 1.095(% water); r = -0.98; R^2 = 0.97; n = 140.

The regression equation for B is:

% lipid = 13.81 - 0.150 (% water); r = -0.70; R^2 = 0.49; n = 59.

The dashed line, C, is the mean percent lipid of the ovaries. The sample size of C is 69.


24
20
16
12
8
4
0
PERCENT LIPID
A
B
C
0
60
64
68
72
76
80
PERCENT WATER

T-tests revealed that there is no difference between the mean energy densities of the soma of males and those of the soma of females for any sample and so the two sets of data were pooled. The annual cycle of mean energy densities of the three compartments are shown in Fig. 7.

In order to determine the energy conversion factors for lipid and solid the percentages were converted to weights and the energy densities to total energies by multiplying the percentages by the wet weight of the tissue. Solid is defined as the residue left after extraction of lipid and water. Then total energy was regressed on the weight of lipid and the weight of solid to obtain the following equations for the soma, the testes and the ovaries respectively:

soma:

(6a) Energy = 50.48 + 38.80 (lipid) + 20.30 (solid)

testes:

(6b) Energy = -1.45 _ 20.59 (lipid) + 22.07 (solid)

ovaries:

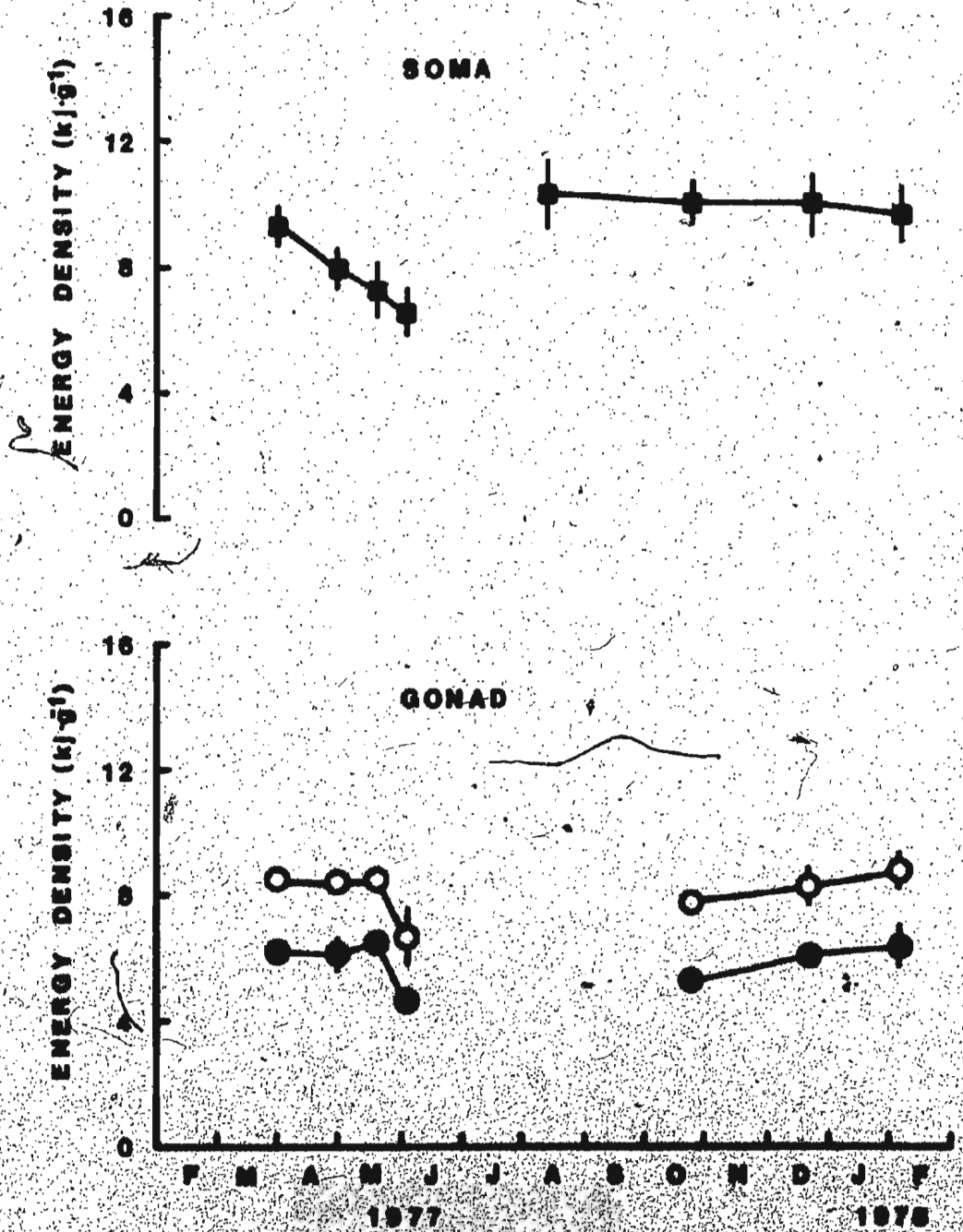
(6c) Energy = 15.80 + 18.13 (lipid) + 25.19 (solid)

The equations are significantly different from each other (t-test, $P < 0.001$). The equation for somatic energy, (6a), was found to be not significantly different (t-test, $P > 0.1$) from the equation,

(7) Energy = 39.75 (lipid) + 20.92 (solid),

The coefficients in equation (7) are those commonly used in the ecological literature (1 g lipid = 9500 cal = 39.75 kj;

Fig. 7. The annual cycle of the mean (± 1 s.d.) energy density of the soma, the testes and the ovaries. The gonads of the specimens of the August 12 sample were sexed incorrectly and were therefore omitted. The open circles are females, the closed circles are males and the squares are pooled males and females.


SOMA
GONAD
ENERGY DENSITY (kJ·g⁻¹)
16
12
8
4
0
F M A M J J A S O N D J F
1977
1978

1 g solid = 5000 cal = 20.92 kj) (Beamish et al. 1975). However, both equations (6b) and (6c) are significantly different from equation (7) ($P < 0.001$). The use of equations (6b) and (6c) introduces a 4.42% and an 11.79% error, respectively, in the estimation of total energy.

The energy density of a tissue can be estimated by determining the percent water content and then by substituting that value into equations (5) and (6). The calculations can be simplified by deriving one expression for the dependence of energy density on percent water. Energy density was regressed on percent water to obtain the following equations for the soma, the testes and the ovaries respectively:

soma:

(8a) Energy density = 36.17 - 0.400 (% water)

testes:

(8b) Energy density = 24.08 - 0.248 (% water)

ovary:

(8c) Energy density = 25.52 - 0.260 (% water)

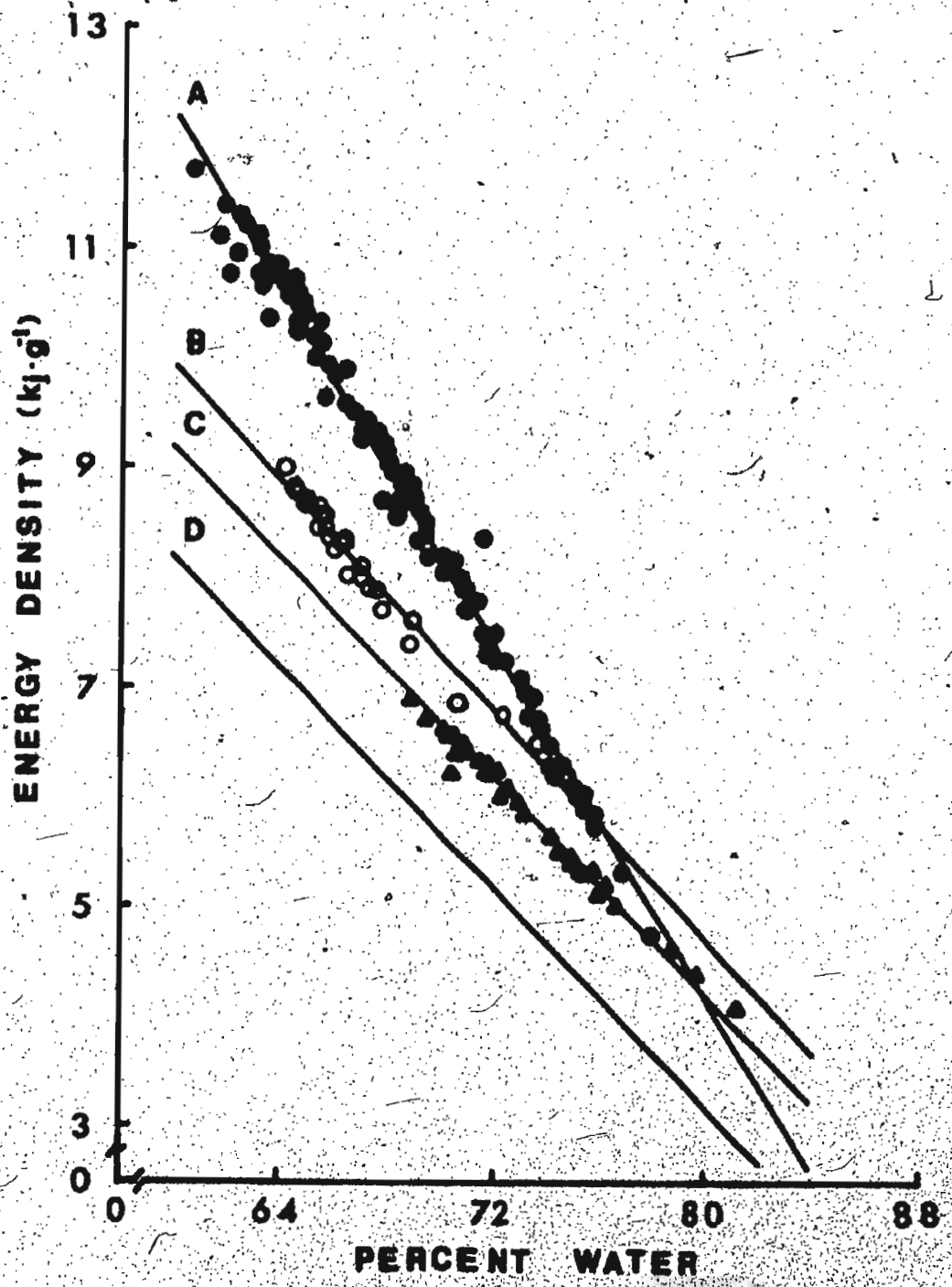
The slopes and the elevations of all three lines are significantly different from each other (t-test, $p < 0.001$). The lines are shown in Fig. 8. Kitchell et al. (1977b) derived a linear regression between energy density and percent water using data from the literature and their line is presented for comparison.

Fig. 8. The relationship between the energy density and the percent water of: A, the soma of the combined sexes; B, the ovaries and C, the testes. The line from Kitchell *et al.* (1977b), D, is presented for comparison. The regression equation of A, B and C are, respectively:

Energy Density = 36.172 - 0.400 (% water); r = -0.99; R^2 = 0.99, n = 121.

Energy Density = 25.522 - 0.260 (% water); r = -0.99; R^2 = 0.99, n = 43.

Energy Density = 24.082 - 0.248 (% water); r = -0.99; R^2 = 0.98; n = 48.


13
11
9
7
5
3
0
ENERGY DENSITY (kj·g⁻¹)
A
B
C
D
0
64
72
80
88
PERCENT WATER

Discussion

There is a continuous decrease in the body condition index and the somatic energy density of the Atlantic herring throughout the winter and spring. If one assumes, as did Winters (1977), that overwintering herring of the Newfoundland area feed negligibly or not at all then this loss of body weight and somatic energy density represents energy expended in metabolism. Making this assumption Winters (1977) calculated a mean overwintering metabolic rate of Atlantic herring (see p.42).

The significantly higher mean body condition index of the males compared to that of the females of the October 25 sample is most probably the result of the fact that the testes grow faster than the ovaries (Table II and Figs. 2B and 2C). This sexual difference in the scheduling of gonad growth is a phenomenon that has also been observed in North Sea herring (Iles 1964). It can be speculated that the testes begin growth sooner than the ovary because the male has a higher total body energy content than the female after spawning. The testes, being approximately half as energy rich as the ovaries would represent less of an energy drain to the pre-spawning male than the ovaries do to a pre-spawning female. This implies that a threshold of body energy exists above which gonad growth is possible but below which gonad growth is suppressed. One piece of supporting evidence for this hypothesis is the observation by Wilkins (1967) that juvenile Atlantic herring that had been starved for four months in captivity did not undergo sexual maturation,

whereas their wild counterparts had begun to mature sexually during that period.

There is a large body of data on the seasonal cycle of the percent lipid and the percent water of the flesh and the gonads of many species of fish. Herring have been particularly well studied in this respect (reviewed by McBride et al. 1959, Leim 1957, 1958; Stoddard 1967, 1968; Hodder et al. 1973; Ackman and Eaton 1976; Varga et al. 1977). There is general agreement among the aforementioned that the percent lipid of the herring tissue varies seasonally depending upon the amount of food available and upon the state of maturation of the gonads. There is also agreement that the percent lipid and the percent water of the flesh vary inversely with each other and that the percent solid varies little with season.

Hodder et al. (1973) found no correlation between the precent lipid and the length of the fish, which is in agreement with this study (Table VI). They did, however, find that, on the average, females have a 5% higher absolute lipid content than males over the entire range of the lipid content values. It was not tested to determine if there is a statistically significant difference. No significant differences in percent lipid and percent water between sexes were found in this study. Perhaps the 5% difference is related to the sampling method, Hodder et al. (1973) per-

formed whole body analysis while this study considers the body as three separate compartments.

The reported seasonal cycle of percent lipid of Hodder et. al. (1973) is virtually identical to that reported here (Fig. 5); a maximum of approximately 15% in January and a minimum of approximately 6% in June, immediately after spawning. They also reported that the lipid/water relationship did not appear to be strictly linear and so fitted the data with a second degree polynomial regression. Since equation (5a) has a very high correlation coefficient ($r = -0.98$) (Fig. 6) and it explains 98% of the variance of the data it is not considered necessary to attempt to improve the fit by using polynomial regression.

The energy density of a tissue can be determined directly by bomb calorimetry or indirectly by conversion of the weights of lipid and solid to energy units with standard energy density factors. The energy density of lipid is commonly reported as 38.91 - 39.75 kj $\cdot$ g^{-1} (Beamish et al. 1975). However, Niimi (1972, referenced in Beamish et al. 1975) reports a value of 35.56 kj $\cdot$ g^{-1} which suggests that the value should be revised or at least reexamined. Also, since solids can consist of differing proportions of protein (23.64 kj $\cdot$ g^{-1}), carbohydrate (16.74 kj $\cdot$ g^{-1}) and ash the energy density coefficient of solid of 20.92 kj $\cdot$ g^{-1} can serve only as a mean value. These standard factors are appropriate for determining the energy content of herring

soma but introduce error if used to determine that of the gonads. This is likely due to the difference in the proportions of protein and other solids in the soma and the gonads.

The significant differences between equations (8a), (8b) and (8c) can be explained as due to the differing proportions of lipid, water and solid found in the soma and the gonads. The close fit of these equations ($R^2 = 0.99$) indicates that they can be used to calculate the energy density of a body compartment with high accuracy. Their use would greatly simplify the task of monitoring the energy content of a herring population should such a program be initiated. The greatest source of inaccuracy in the estimates of energy content would lie in the estimation of the compartment weights.

Kitchell et al. (1977b) proposed the following relationship between the energy density and the percent water of fish flesh:

$$\text{Energy density} = 23.17 - 0.25(\% \text{ water}).$$

The slope of the regression is almost indistinguishable from that of equations (8b) and (8c) but is quite different from equation (8a), (Fig. 8). Both (8b) and (8c) have a higher elevation than Kitchell's regression and this is almost certainly due to the fact that many of Kitchell's samples were whole-body samples which include bone. This would tend to lower the energy density of a sample and therefore lower the elevation of Kitchell's regression. The

reason for the higher slope of equation (8a), 0.400 as compared to 0.25, lies in the life-history of the herring. It must store large amounts of energy in the form of lipid in its musculature in order to survive long periods of non-feeding. Therefore the seasonal change in the energy density of the herring soma is greater than most fish, especially if one considers tropical fish such as tuna as did Kitchell et al. (1977b).

PART II

Model Description

Kerr (1971), Beamish et al. (1975) and Jones (1976) should be consulted for a review of the development of piscine energetics models.

The energy balance equation (Winberg 1956) is

(9) $$e_r R = M + \Delta E$$

where R is the rate of rations intake, e_r is the coefficient of utilization of the rations, M is the metabolic rate and ΔE is the change in energy content of the body.

The metabolic rate can be broken down into four compartments: M_s, the standard metabolic rate; M_{sa}, the metabolic expenditure of spontaneous activity; M_{sda}, the metabolic rate accounted for by specific dynamic action (SDA) and M_f, the metabolic expenditure of foraging activity,

(10) $$M = M_s + M_{sa} + M_{sda} + M_f.$$

The routine metabolic rate of most fish, including herring, is the sum of M_s and M_{sa}. This can be expressed as

(11) $$M_s + M_{sa} = \alpha W^{\beta} Q(T)$$

where α is the level of metabolism, β is the weight exponent, T is temperature and Q(T) is a temperature correction factor derived from Krogh's empirical temperature correction curve

(Winberg 1956).

M_{sda} can be most conveniently expressed as

(12) $$M_{sda} = mR$$

where m is the SDA coefficient (Kerr 1971; Ware 1975).

M_f can be calculated two ways: by using basic hydrodynamic principles (Ware 1978; Sharp and Francis 1976) or by assuming it is directly proportional to the routine metabolic rate (Winberg 1956; MacKinnon 1973; Laurence 1977). The former approach requires a number of empirical coefficients the values of which should, ideally, be derived from laboratory studies of respiration rate. Since this data is unavailable for herring the first approach cannot be used. Instead, M_f is calculated as

(13) $$M_f = A(M_s + M_{sa})$$

where A is the activity coefficient.

The change in stored body energy can be divided into the change in energy content of the soma, ΔE_s, the change in energy content of the gonads, ΔE_g, and the change in energy content of the head, ΔE_h,

(14) $$\Delta E = \Delta E_s + \Delta E_g + \Delta E_h.$$

The change in energy content of a compartment is calculated as

(15) $$E_t = c_t W_t - c_{t-1} W_{t-1}$$

where c is the energy density and t is time. The head is

assumed to have a constant energy density because of the absence of any lipid storage depots.

The gonad weights are calculated using the annual cycle of mean gonad condition indices. The ovary condition index is corrected for the effects of age by using equation (4b), i.e.

$$I_o = \bar{I}_o + 0.0094(\text{Age}) - 0.0835 \tag{16}$$

where $\bar{I}_o$ is the mean ovary condition index. In order to prevent $\bar{I}_o$ from becoming a negative number immediately after spawning it is further adjusted by multiplying the age correction factor by the ratio of $\bar{I}_o$ to the maximum mean ovary condition index, $\bar{I}_o^*$.

$$I_o = \bar{I}_o + (0.0094(\text{Age}) - 0.0835)\bar{I}_o/\bar{I}_o^* \tag{17}$$

In the same manner the body weight is calculated using the annual cycle of mean body condition index, $\bar{C}$, corrected for age with equation (4a) and adjusted by the ratio of the mean ovary condition index to $\bar{I}_o^*$.

$$C = \bar{C} + (0.066(\text{Age}) - 0.5105)\bar{I}_o/\bar{I}_o^* \tag{18}$$

The reasoning behind the use of the ovary condition index ratio in equation (18) is that the increase in body condition index with age represents the increase in gonad condition index and not an increase in somatic condition index. Therefore the age adjustment of $\bar{C}$ must track the seasonal cycle of I_o.

The head weight is calculated from a regression of

head weight, W_h, on body length,

(19) $$W_h = 7.8 \times 10^{-7} L^{2.966}; \; r = 0.90; \; R^2 = 0.8$$

The length is calculated from

(20) $$L_t = L_{t-1} + (\Delta L)_t$$

Where $(\Delta L)_t$ is an increment of length.

To summarize, the model can be written as

(21) $$R = \frac{1}{e_r - m} (\alpha W^{\beta} Q(T)(A + 1) + \Delta E_s + \Delta E_g + \Delta E_h).$$

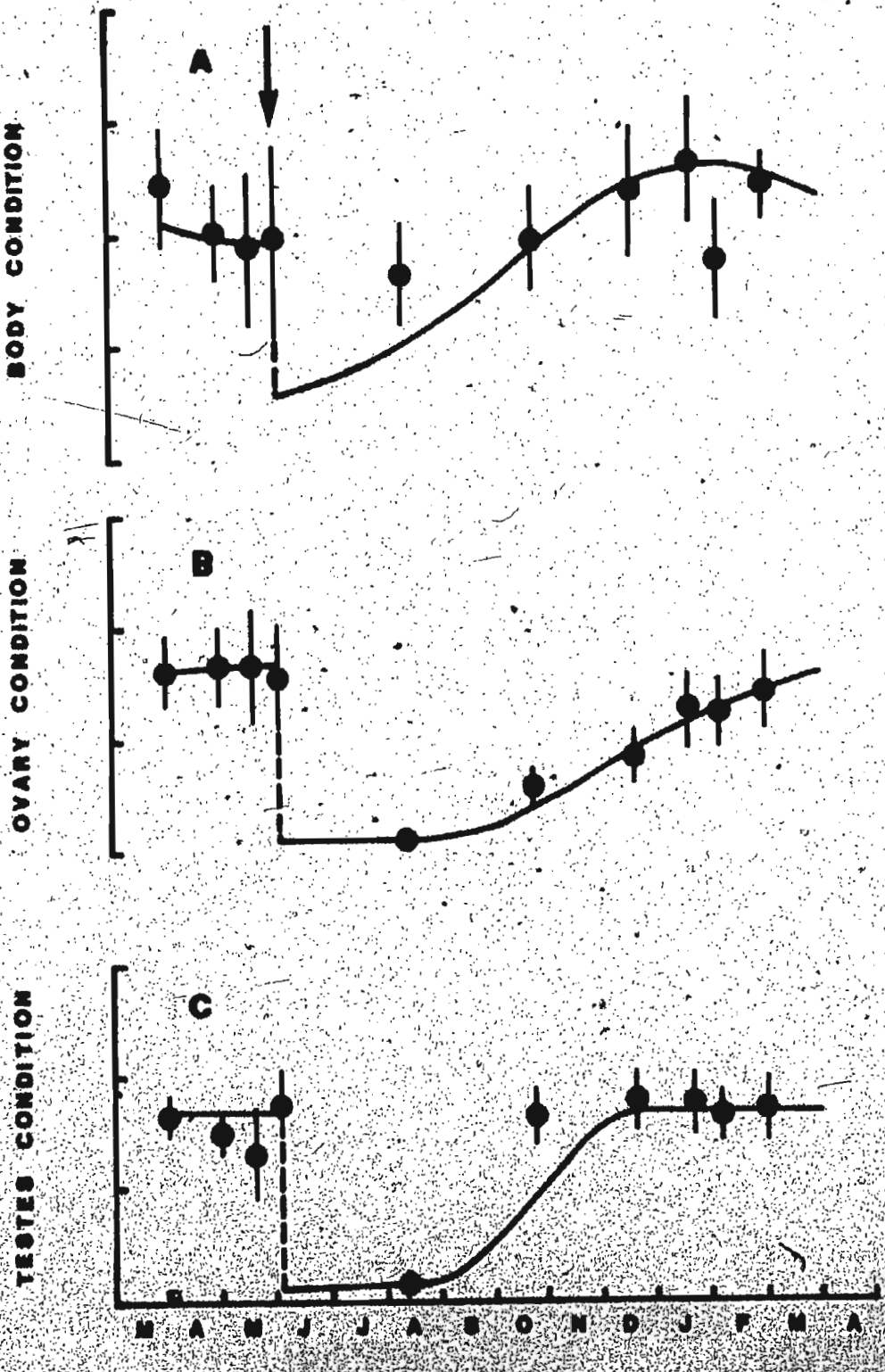
Data and Parameters

The model begins on April 1 and simulates a time period of one year in increments of one week. The beginning data was chosen so that the energy density data could be used directly in the model. The output is a listing of the length, the weights and the rates of energy storage and depletion for each week. The age of sexual maturation is assumed to be three and the gonad is assumed to lose 90% of its weight during spawning.

The weekly values of the energy densities, the body condition index, the gonad condition indices and the growth increments were obtained by fitting smooth curves by eye to the data. The curves were further smoothed by taking a running average of 3. All fish whose measurements were used were caught between March 1976 and March 1977. The growing season is assumed, on the basis of data on the feeding intensity of herring, to start April 1 and end November 1 (G. Winters, personal communication) and the growth pattern is assumed to be sigmoid.

The condition index curves used in the model are shown in Fig. 9. The body condition index curve is drawn beneath the point representing the mean of the August 12 sample because it is felt that it is unlikely that the herring could regain body condition so quickly after spawning. It is possible that the specimens of the August 12 sample were early spawners. The drop in body condition index, represented by the dotted line, was calculated, as in Fig. 2,

Fig. 9. Seasonal cycle of condition indices used in the model: A, the body; B, the ovary; C, the testes. The bars represent ± 1 s.d. The curves were drawn by eye and then smoothed by taking a running average of three. The arrow indicates the mean date of spawning.


A
BODY CONDITION
B
OVARY CONDITION
C
TESTES CONDITION
M A M J J A S O N D J F M A

by subtracting the mean gonad weight at spawning from the mean body weight at spawning.

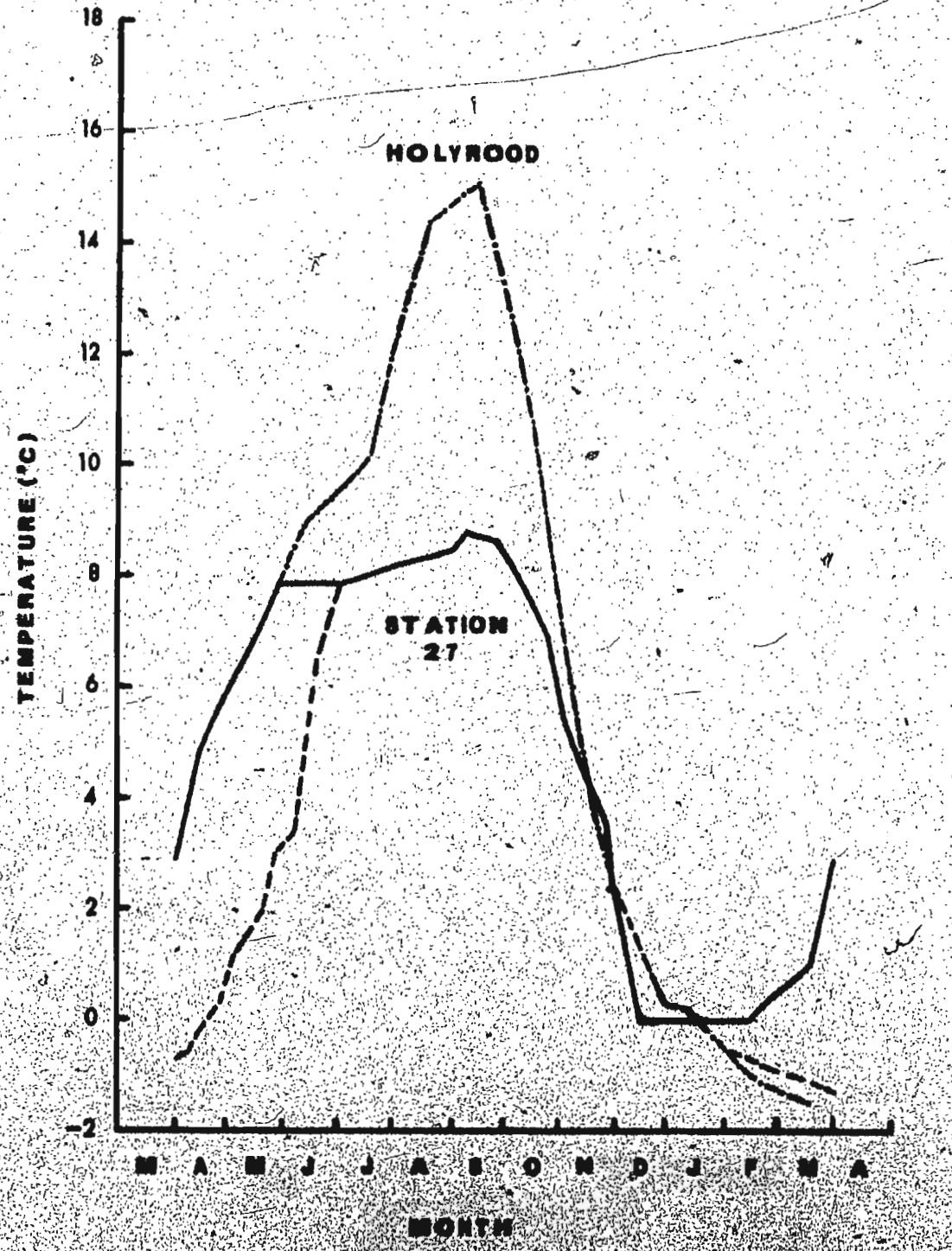
The annual growth increments were obtained from the same data by fitting the von Bertalanffy equation

$$L = L_{\infty} (1 - e^{-K(t - t_0)}) \quad (22)$$

where L_{∞} is the length at infinity, K is the instantaneous growth rate and t_0 is the hypothetical time when length would have been zero if K was constant throughout the fish's lifetime. The parameter values were calculated by Beverton's method (Ricker 1975) and are shown in Table VII.

Since herring overwinter in inshore waters and, presumably, feed in offshore waters the seasonal water temperature curve must be a composite of both the inshore and the offshore water temperature curves. Fig. 10 shows the curve for surface water at Holyrood, at the head of Conception Bay (Steele 1974), and the curve for Station 27 (supplied by the courtesy of D. McKone, Biological Station, St. John's, Newfoundland), an oceanographic sampling site in the Atlantic east of the Avalon Peninsula. The latter curve is the mean temperature of the water above the thermocline. The curve used in the model follows the Holyrood curve until May 30 at which time it shifts to the Station 27 curve until November 1 at which time it shifts back to the Holyrood curve. It is constrained to be greater than or equal to zero because it is felt that the herring are unlikely to experience water temperatures below zero.

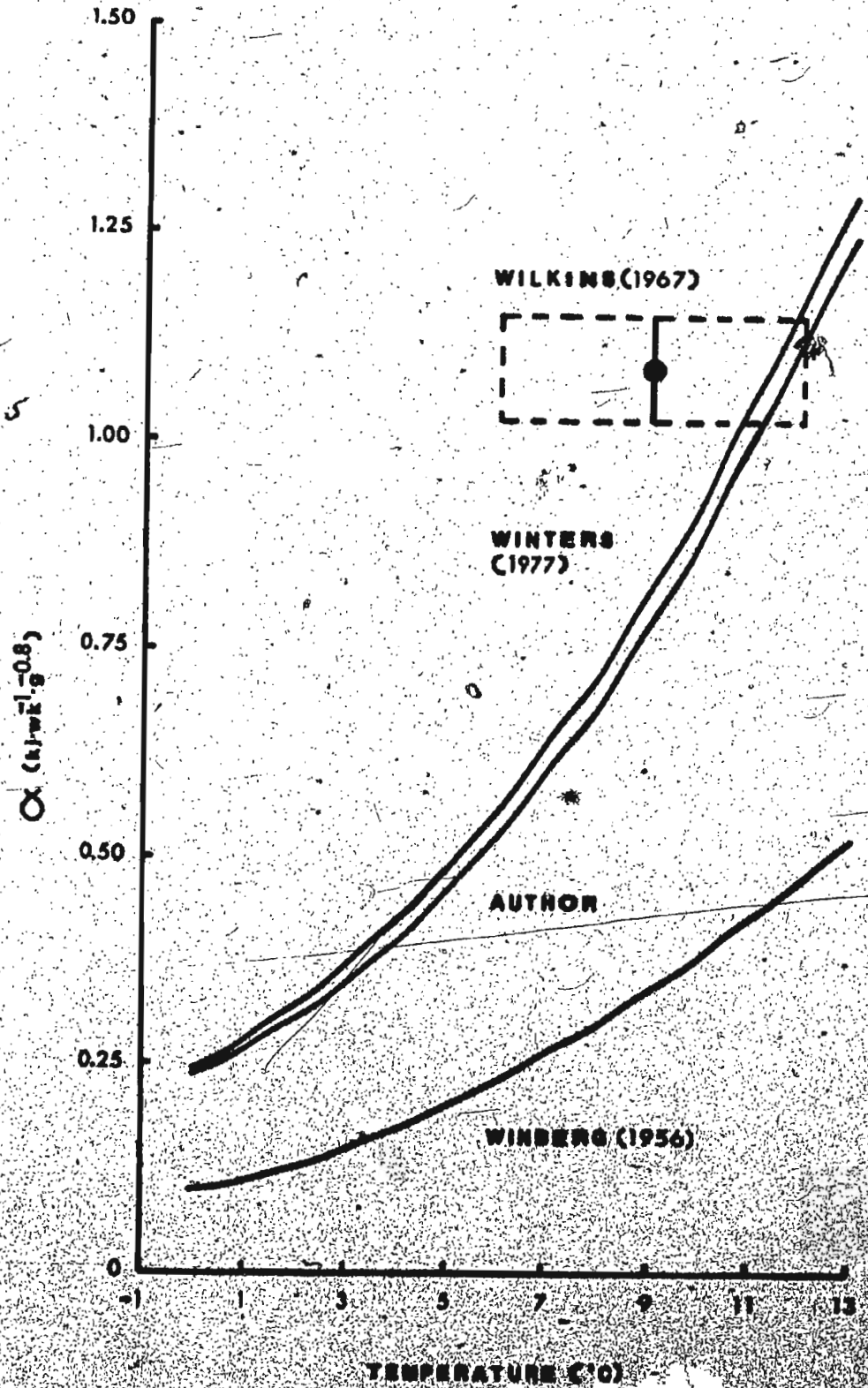
Fig. 10. Monthly water temperatures for Holyrood (Steele, 1974) (-.-.-.) and Station 27 (----). The solid curve is used in the model.


18
16
14
12
10
8
6
4
2
0
-2
TEMPERATURE (°C)
HOLYROOD
STATION 27
M A M J J A S O N D J F M A
MONTH

The food utilization coefficient, e_r, is commonly assigned a value of 0.8 (Winberg 1956) and this is the value used in the model. It is undoubtedly only a mean value since recent work has shown that it varies depending on ration rate and temperature. Elliott (1976) found that the value for brown trout lies between 0.75 and 0.70 and that it decreases with increasing rations rate and increasing temperature. The metabolic weight exponent is also given a mean value of 0.8 (Winberg 1956).

There are no reported direct measurements of α; however, there are two studies available from which indirect estimates can be obtained. Winters (1977) estimated $(M_s + M_{sa})$ for spring-spawning herring 316 g in weight as 0.34 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ at 3 C by measuring the mean loss of body energy of overwintering, non-feeding herring of the south-west Newfoundland stock complex and equating this to metabolic expenditure. This gives an α of 0.37 $kj \cdot wk^{-1} \cdot g^{-0.8}$, assuming 1 ml O_2 is equivalent to 0.0203 kj (Beamish et al. 1975). Applying the same method to the data of this study yields an α of 0.27 $kj \cdot wk^{-1} \cdot g^{-0.8}$ at an estimated mean temperature of 1 C. Wilkins (1967) starved spring-spawning herring caught in the Firth of Clyde and reported the changes in proximate composition of the fillets and the changes in body weight. Utilizing equation (6a) the α was calculated as 1.02 - 1.14 $kj \cdot ek^{-1} \cdot g^{-0.8}$ over a temperature range of 6-12 C. The three estimates are shown in Fig. 11. The curves were calculated using the coefficients of Krogh's temperature

Fig. 11. Values for the level of metabolism, α, as a function of temperature. The curves were calculated using Krogh's correction curve. The curve labelled Author was derived from this study and is used in the model.


1.50
1.25
1.00
0.75
0.50
0.25
0
WILKINS (1967)
WINTERS (1977)
AUTHOR
WINBERG (1956)
-1
1
3
5
7
9
11
13
TEMPERATURE (°C)

correction curve presented in Table 1 of Winberg (1956). The estimate derived from Wilkins' data is not corrected for temperature due to the large variability in the value but is included for comparison. Winberg's estimate of α is also included for comparison. It is substantially lower than any of the others but this is not unexpected since Winberg's equation, $0.3W^{0.8}$ ml $O_2 \cdot g^{-1} \cdot h^{-1}$, calculates low routine metabolic rate whereas herring are always quite active. Since the α obtained from this study is within the range of the other two estimates it is used in the model.

There are two direct studies and one indirect study that give experimentally derived values for m, the SDA coefficient. Beamish (1974) found a mean ($\pm$ 1 s.d.) value of 0.142 ± 0.042 for largemouth bass, Micropterus salmoides, fed emerald shiners. This value was independent of feeding level or body weight. Muir and Niimi (1972) determined a value of 0.16 for the aholehole, Kuhlia sandvicensis, fed tuna. Ware (1975) calculated m to be 0.16 in an indirect manner by applying SDA factors for fat, protein and carbohydrate to data on the proximate composition of copepods. An SDA factor is the fraction of the total food energy released as heat when a component such as fat, protein or carbohydrate, is fed separately or in combination. It appears, then that assigning a mean value to m of 0.15 is not unreasonable.

Winberg (1956) proposed that doubling M_s is a reasonable estimate of the metabolic rate of an active fish and Ware (1975) proposed that tripling M_s is a more accurate

estimate for young, highly active fishes. A, the foraging activity parameter, is analogous to these multipliers but not identical unless it is assumed that the routine metabolic rate for herring is equivalent to the M_s of other species. In this model A is assigned values that maintain rations at zero or greater throughout the year. In this way A is almost identical to a_1, a metabolic constant of MacKinnon's (1973) energetics model which was used to adjust the activity metabolism so that the overwintering rations rate was equal to zero. A is 1 during the feeding season (April 1 - November 1) and 0 at all other times.

There is both theoretical and experimental evidence to support the choice of these particular values of A. Ware (1975) proposed that if foraging fish swim at a rate that maximizes their growth rate the ratio of the total metabolism to the routine metabolism should fluctuate between 1.5 and 2.5. In other words, the total metabolic rate of a foraging fish should have a mean value twice that of the routine metabolic rate, i.e. A = 1.

DeSilva and Balbontin (1974) kept young herring in large tanks (750 l) at different temperature and ration levels in order to estimate food intake and growth efficiency. The ration rate and the estimated metabolic expenditure of fish fed to satiation twice a day at 14.5 C were regressed on body weight to obtain the following equations:

$$R = 1.465W^{0.744}$$

$$M = 1.003W^{0.773}$$

where R and M are in units of g food·fish^{-1}·wk^{-1}. A value of A can be calculated, first, by converting the weight of food into energy units by using an energy density constant, c'. This constant has a value of 3.82 kj·g^{-1} and was derived by applying energy density data from Thayer et. al. (1973) and Cummins (1971) to a mussell: squid:mysid diet of proportions 0.125:0.375:0.500. Then the above equations and equation (12) were substituted into equation (10) to give

$$c'(1.003W^{0.773}) = M_s + M_{sa} + mc'(1.465W^{0.744}) + M_f.$$

When equations (11) and (13) are substituted

$$c'(1.003W^{0.773}) = \alpha W^{\beta} Q(T)(A + 1) + mc'(1.465W^{0.744})$$

and A = 0.81.

The parameter values used in the model are listed in Table VII.

Table VII Parameter values for the energetics model of Atlantic herring(Clupea harengus harengus).

Parameter	Symbol	Value
The level of metabolic rate at 20°C	α	0.27 $kj \cdot wk^{-1} \cdot g^{-0.8}$
The weight exponent of metabolic rate	β	0.80
The coefficient of activity metabolism	A	1.0/0.0
The SDA coefficient	m	0.15
The coefficient of utilization of rations	e_r	0.80
The length at infinity	L	352 mm
The instantaneous growth rate	K	0.62 yr^{-1}
The hypothetical time when L = 0	t_o	0.54 yr

Model Results

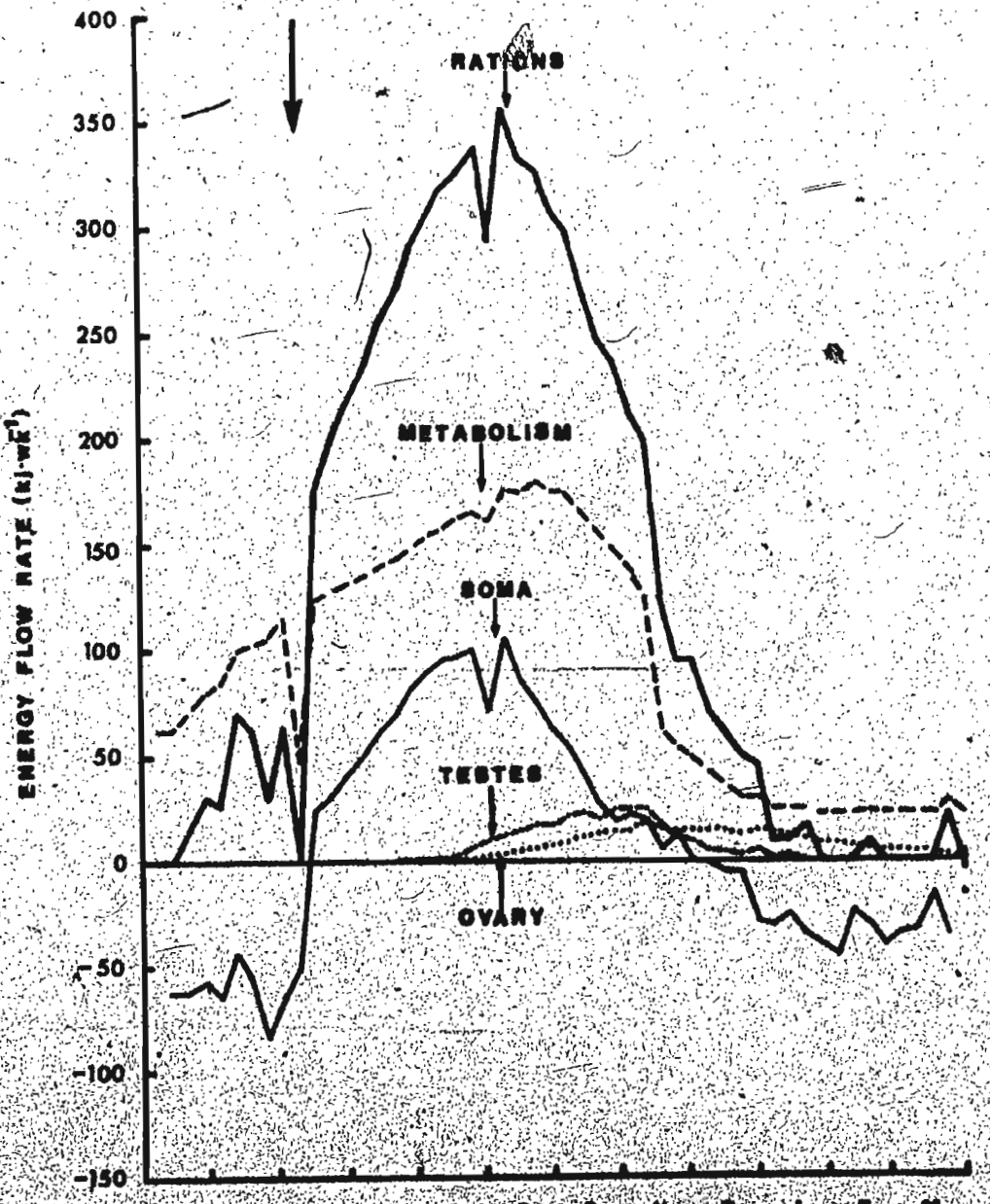
Seasonal Energy Flow

The seasonal pattern of energy storage and depletion rates of a 4 - 5 year old herring is shown in Fig. 12. The head energy flow rate is not shown because of its small magnitude. The maximum ration rate and somatic growth rate occur in late summer, approximately four months after spawning. The maximum somatic degrowth rate occurs in May. The gonads remain dormant until August and then commence growth. The growth rate of the testes rapidly increases to a maximum in late October and then decreases to zero in January, whereas that of the ovary is low but steady throughout the winter with a broad peak in November and December.

Herring are not assumed to feed during the spawning period (G. Winters personal communication). This behavioural phenomenon is mimicked in the model by setting $(\Delta L)_t$ and A to zero for the spawning period.

The seasonal pattern of metabolic expenditure for a 4 - 5 year old herring is shown in Fig. 13. It obviously follows the temperature curve very closely. The slight upward trend of routine metabolic rate ($M_s + M_{sa}$) is due to the increasing weight of the fish over the growing season. The sudden drop in early November is due to the transition of A from a value of 1.0 to 0.0 and is undoubtedly unrealistic in its magnitude. The shape of the curve of M_{SDA} is, of course, a low amplitude replica of the rations rate curve.

Fig. 12. The seasonal pattern of energy storage and depletion of a 4-5 year old herring. The large arrow indicates the time of spawning.


400
350
300
250
200
150
100
50
0
-50
-100
-150
ENERGY FLOW RATE (kJ·wk⁻¹)
RATIONS
METABOLISM
SOMA
TESTES
OVARY
A
M
J
J
A
S
O
N
D
J
F
M

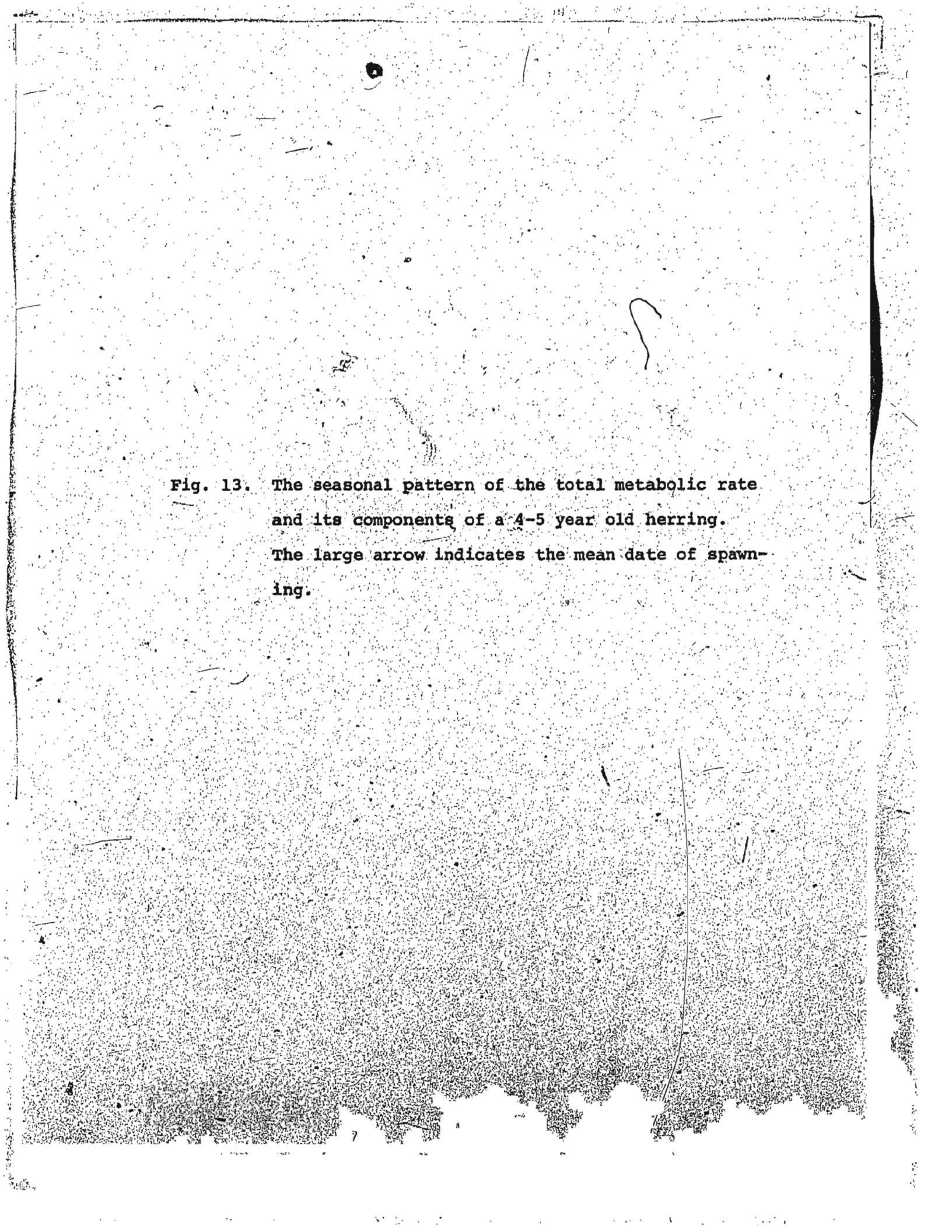
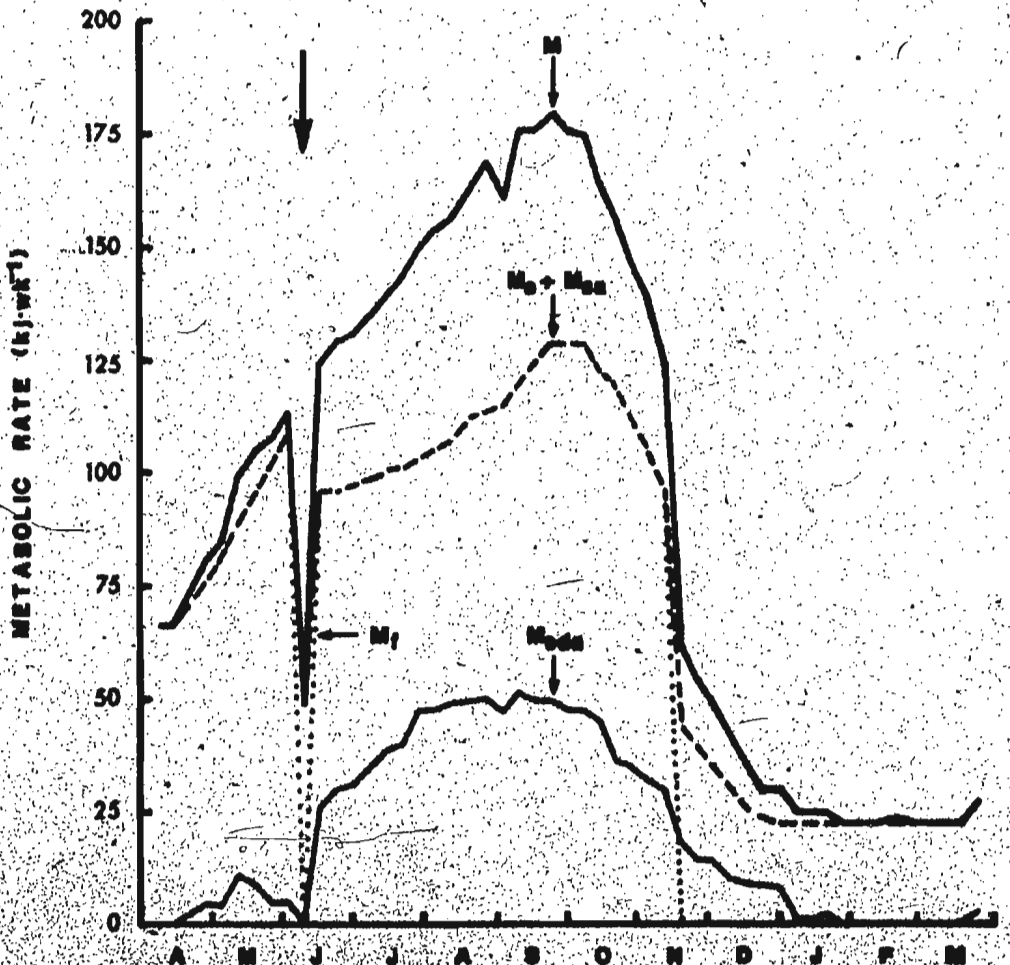


Fig. 13. The seasonal pattern of the total metabolic rate and its components of a 4-5 year old herring. The large arrow indicates the mean date of spawning.


200
175
150
125
100
75
50
25
0
A
M
J
J
A
S
O
N
D
J
F
M

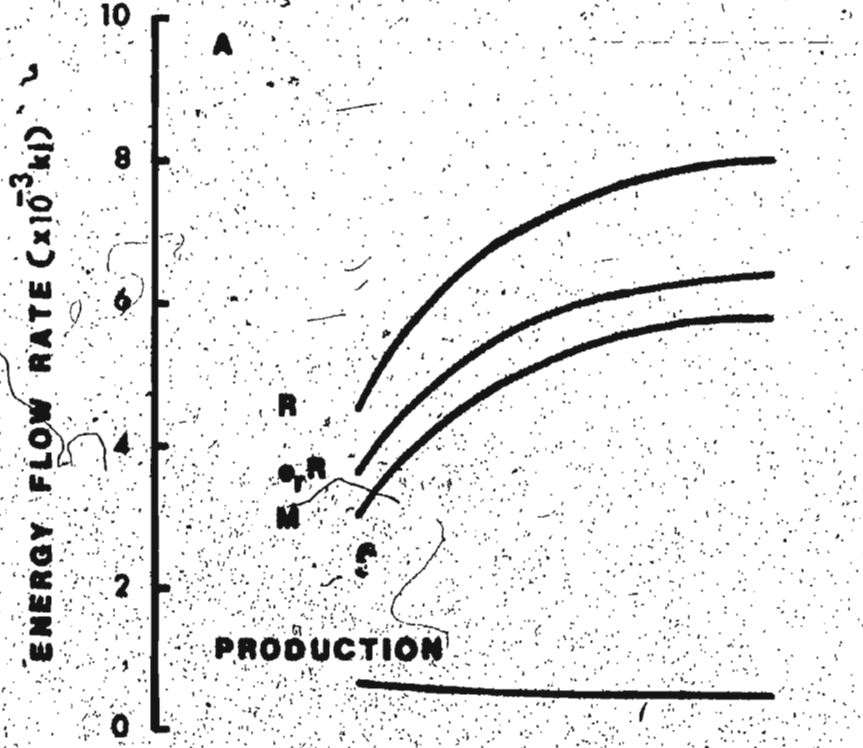
Age Distributions

The distribution of energy flow rates with age is shown in Fig. 14A. The metabolic rate utilizes the greatest portion, 81.1% - 91.8%, of the assimilated rations at all ages, with the percentage increasing with age. This results in a decreasing rate of production as progressively less energy is available for either somatic or gonad growth. An additional characteristic of this system is that the gonad growth rate takes an increasingly larger share of the decreasing growth-related energy flow rate. This results in a precipitous decline in the somatic growth rate with age. This phenomena is shown for a female herring in Fig. 14B.

The modelled fecundity is shown in relation to the mean weight and the mean length at age in Fig. 15. The mean length and weight were calculated by summing the weekly values and dividing by 52. The fecundity was regressed on weight and length using the logarithmic transformation. This transformation was chosen because it is most often used by other workers but inspection of Fig. 15 shows that the points are not fitted well and it is possible that another model, perhaps polynomial regression, could produce a better fit.

The total production rate and its components are shown as fractions of the total annual rations rate for each age, the so-called gross growth efficiencies or K_1 values (Paloheimo and Dickie 1966) in Fig. 16. Finally, the log of the annual rations rate was regressed on the log of the mean body weight at age and shown in Fig. 17.

Fig. 14. The age distribution of the energy flow rates of a female herring: A, the major rates. B, the components of the production rate.


A
ENERGY FLOW RATE ($\times 10^{-3}$ kJ)
10
8
6
4
2
0
R
R
M
C
PRODUCTION

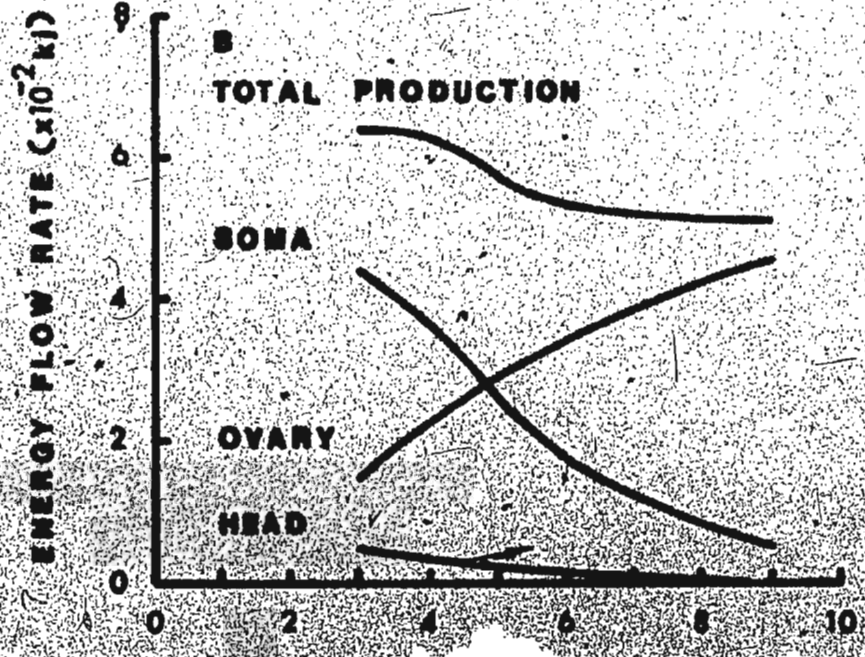
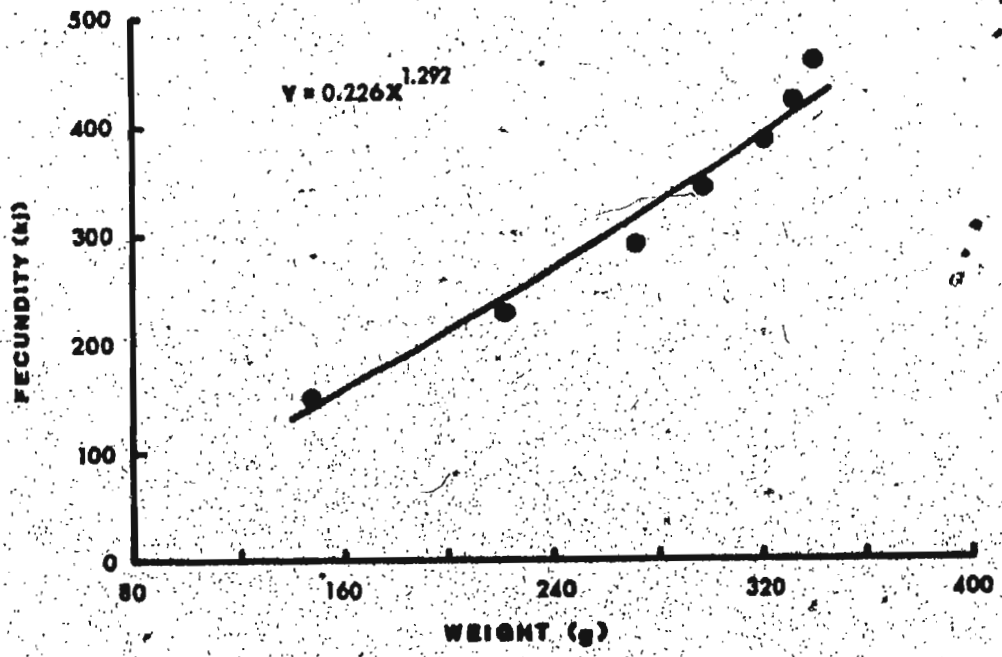

B
ENERGY FLOW RATE ($\times 10^{-2}$ kJ)
8
6
4
2
0
TOTAL PRODUCTION
SOMA
OVARY
HEAD
0
2
4
6
8
10

Fig. 15. The relationship between the modelled fecundity and A, the mean weight at age, and B, the mean length at age.


Y = 0.226X^1.292
FECUNDITY (n)
500
400
300
200
100
0
80
160
240
320
400
WEIGHT (g)

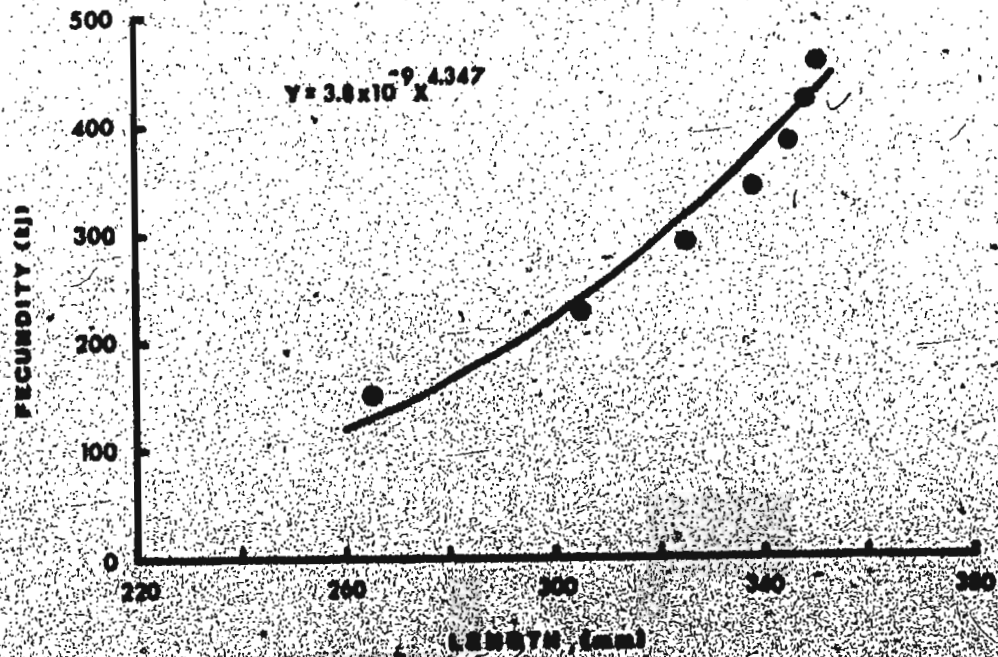
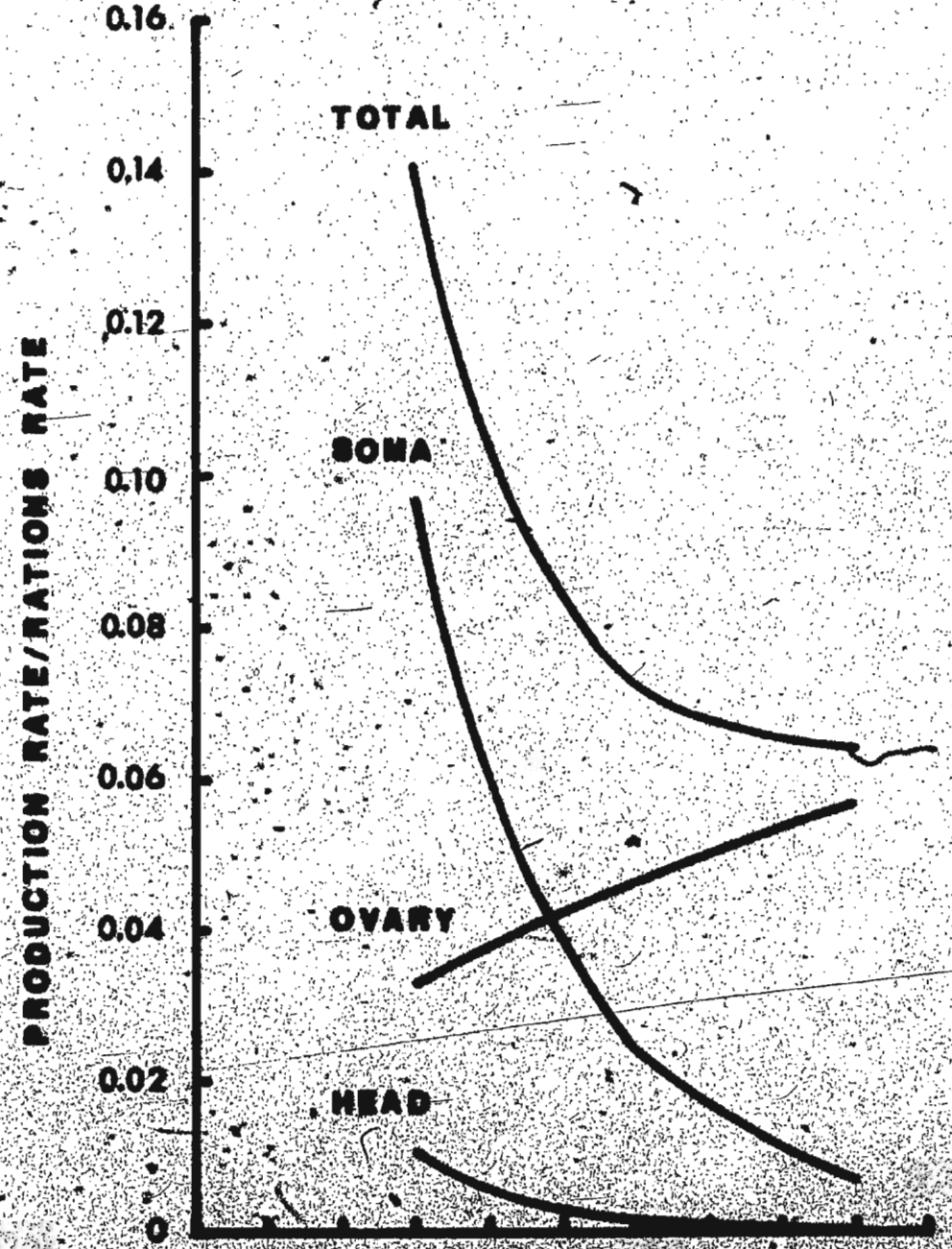

Y = 3.8x10^-9 X^4.347
FECUNDITY (n)
500
400
300
200
100
0
220
260
300
340
380
LENGTH (mm)

Fig. 16. The age distribution of the production to rations rate of the body compartments of a female herring.


0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0
PRODUCTION RATE/RATIONS RATE
TOTAL
SOMA
OVARY
HEAD
0
2
4
6
8
10

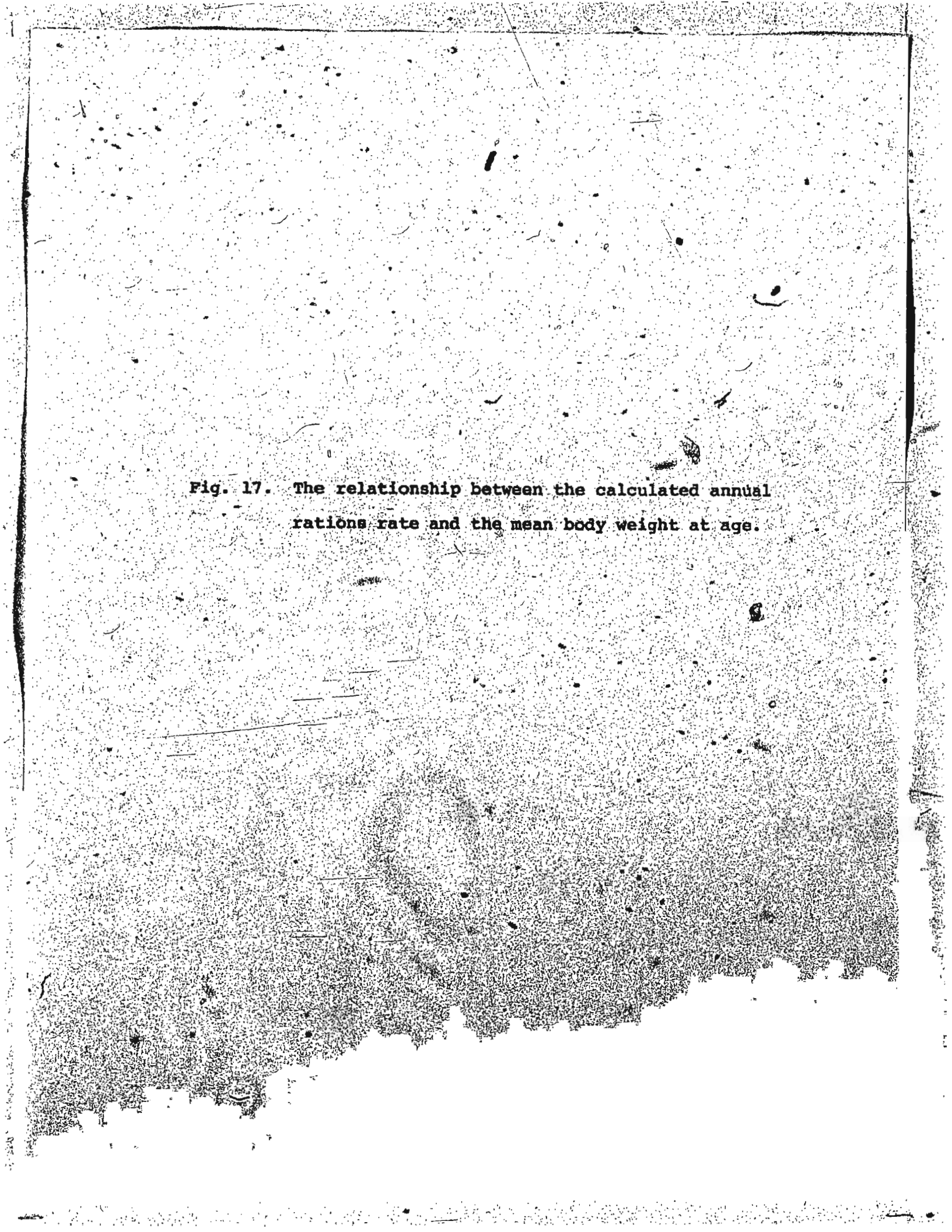
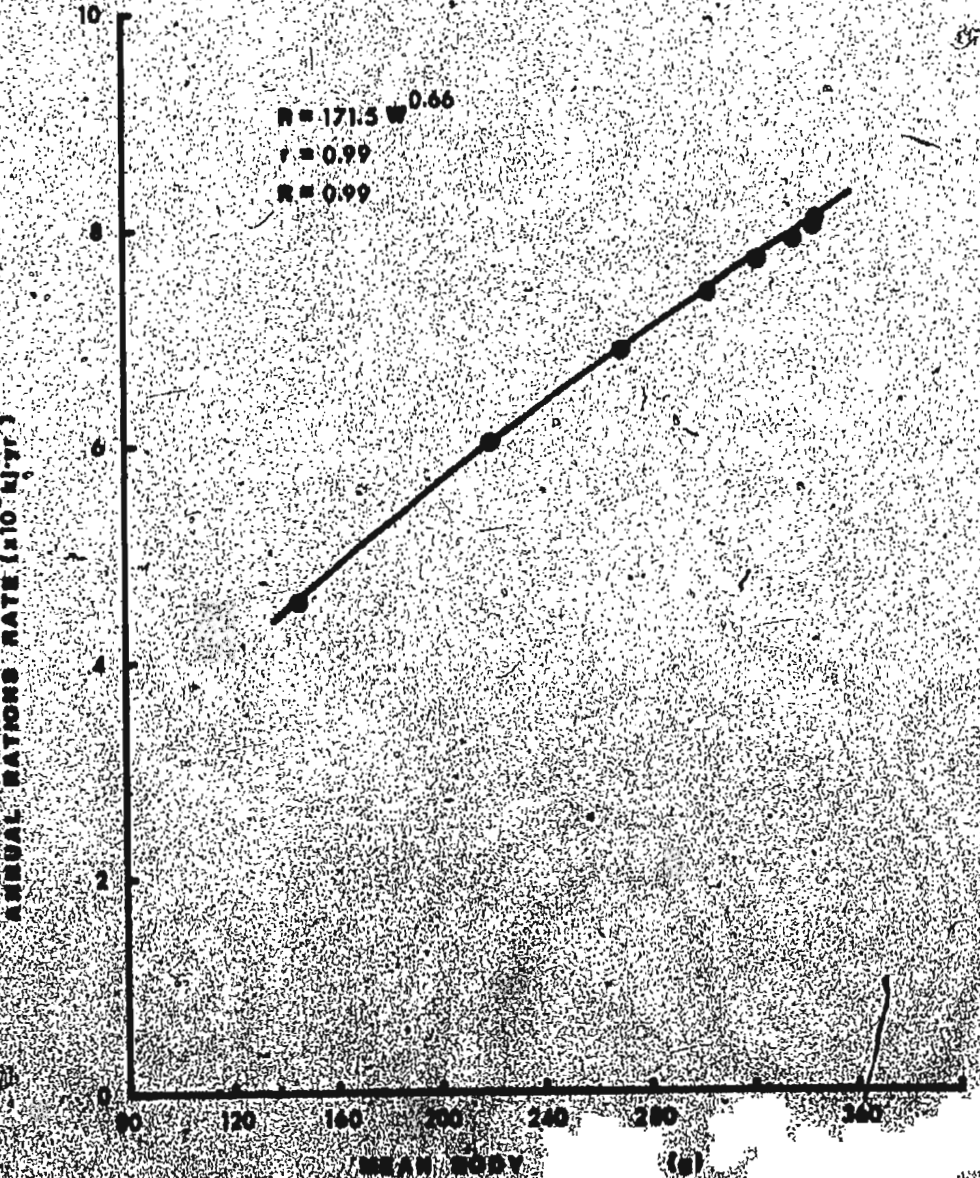


Fig. 17. The relationship between the calculated annual rations rate and the mean body weight at age.


R = 171.5 W^0.66
r = 0.99
R = 0.99
ANNUAL RATIONS RATE (x10^-3 kg kg^-1)
MEAN BODY
(g)
0
2
4
6
8
10
80
120
160
200
240
280
320

Sensitivity Analysis

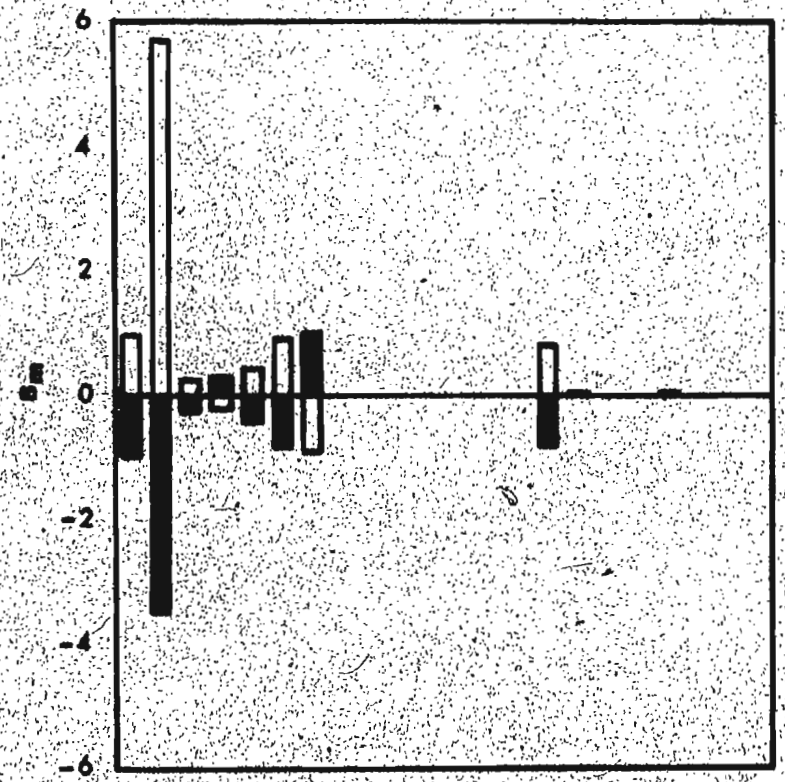
The construction of a model involves a multitude of assumptions, some more questionable than others. A sensitivity analysis was performed in order to examine the consequences of inaccurate data and parameter estimation. This involved altering the assigned values of the data and parameters by 10% and determining the changes in the values of the output variables. The relative sensitivity, S, of a variable y to changes in a parameter or data time series, x, is defined as

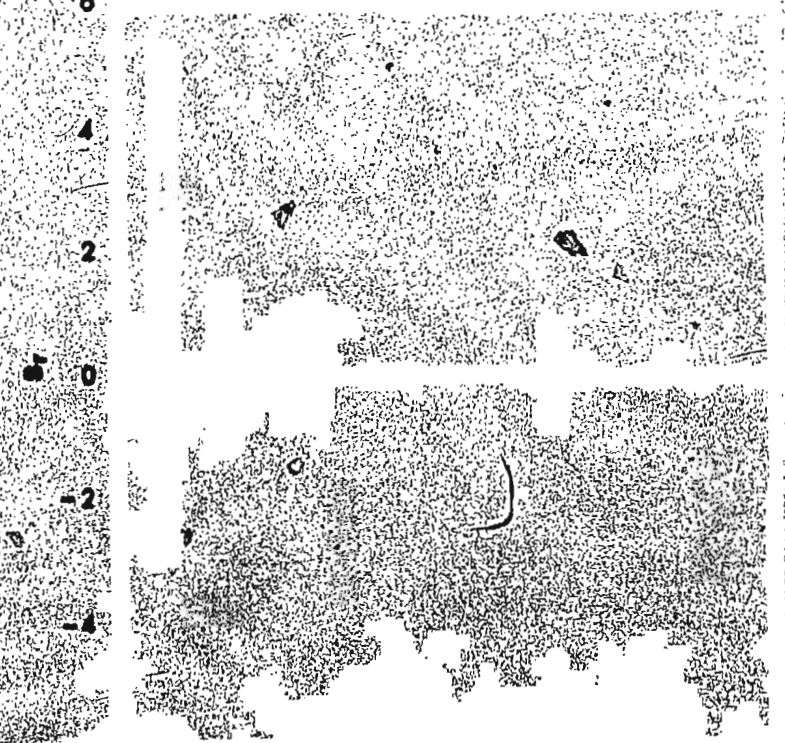
$$S = (\Delta y/y)\ (x/\Delta x) \tag{23}$$

where Δy and Δx are the differences between the original and the altered output variable and parameter, respectively. The sensitivities of the total annual rations rate, S_r, and the total annual metabolic rate, S_m, of a 7 - 8 year old herring are shown in Fig. 18.

The model is most sensitive to changes in α, e_r, β, T and C and least sensitive to changes in $(\Delta L)_t$, I_o, I_t, a_h, b_h, a_b, b_b (the regression constants of the equations used to calculate the head weight and the backbone weight) and the energy densities of the body components. This is fortunate in that the members of the latter group have wide variation associated with them. Also, fortunately, β, the parameter to which the model is most sensitive, is probably the least variable and the most well documented parameter available. Winberg (1956) reports that one standard error

Fig. 18. The sensitivities of the metabolic rate, S_m, and the rations rate, S_r, to the data and parameters. The blackened boxes represent a ΔX of -10% and the open boxes represent a ΔX of +10%.


6
4
2
0
-2
-4
-6


6
4
2
0
-2
-4

of the mean β for a large number of species of freshwater and marine fishes is only 1.75% of the mean.

The parameters that are in need of the most attention are α and e_r. The former because the lack of corroboration renders its derivation suspicious and the latter because it is quite likely that the rate of excretion is not directly proportional to the rations rate.

Energy Allocation Strategies

A growing body of work suggests that the fecundity of a fish is positively correlated with its body condition index and therefore with the rations regime the fish has experienced. There are two hypothesized mechanisms by which the fecundity is adjusted: (i) changes in the rate at which oocytes are recruited to the population of ova; and (ii) follicular atresia, the resorption of already recruited ova. It is possible that either one of these mechanisms may be accompanied by changes in the egg size however, this possibility will not be considered in this study. The second mechanism has been reported to operate in the rainbow-trout, Salmo gairdneri (Scott 1962), the guppy, Lebistes reticulatus (Hester 1964), the brook-trout, Salvelinus fontinalis (Wydoski and Cooper 1966) and the Pacific hake, Merluccius productus (Foucher and Beamish 1977); the first mechanism in the brown trout, Salmo trutta (Bagenal 1969), the gobid Gillichthys mirabilis (DeVlaming 1971) and the winter flounder, Pseudopleuronectes americanus (Tyler and Dunn 1976).

The evidence for fecundity adjustment in herring is

ambiguous. Anokhina (1959, 1971) reports a positive correlation of fecundity with the fat content of fillets of Baltic herring but no correlation for White Sea herring. Instead, for the latter population, fat content is negatively correlated with egg size variability. Hempel (1971) concluded that, ~~at least~~ in some populations, fecundity varies within genetically fixed limits from year to year, depending on the feeding conditions. Zijlstra (1973), on the other hand, found that, for two separate North Sea populations, fecundity does not vary greatly between years and within a year it was not related to the condition of the parent female. If herring fecundity is dependent on the available energy for growth then the mechanism of adjustment of egg number is most likely to be follicular atresia; Bowers and Holliday (1961) observed instances of "pre-ovulatory degeneration" of eggs in a histological survey of the herring gonad.

The question of energy allocation strategies was addressed specifically by Tyler and Dunn (1976). They found a negative correlation between the body condition index and the percent of oocytes not in vitellogenesis. This correlation was observed in both laboratory-reared fish and in flounders sampled in the field. This was interpreted to mean that in times of food scarcity the winter flounder follows a strategy of suppressing gonad growth rather than drawing on body energy reserves. This, supposedly, would enable the fish to maintain body weight which would, in turn, increase the probability of survival and also enable it to produce a

greater number of eggs should the food supply increase in the future.

Three strategies can be proposed: (1) gonad production is maximized at all levels of rations, (2) somatic production is maximized at all levels of rations with gonad growth maintained at a mean level and (3) gonad growth is maximized when rations are high but suppressed in favour of maintaining body weight when rations are low.

The relative fitness of herring following any one of these strategies can be defined as the energy equivalent of the total lifetime fecundity of a female. It serves as an approximation to an ideal fitness index which would measure the number of offspring surviving to the age of sexual maturation. The use of an energy equivalent removes the need to assume a constant survival rate for eggs. The question of whether the energy is distributed into a few, large eggs or many, small eggs will not be examined here.

In nature the level of food availability will fluctuate in response to changes in climate and changes in the intensity of intra- and interspecific competition. To introduce realism into the modelled rations regime the annual fluctuations are assumed to be random and normally distributed. The food availability can be considered to be the sum of multiple independent, random factors operating in series and the Central Limit Theorem of Statistics dictates that it should be normally distributed. Therefore the 'new' rations regime can be recalculated as

(24) $$R' = (1 + \delta)R$$

Where δ is a pesudo-random, normally distributed number with a mean of 0 and a standard deviation of 0.1. The body length and weights of the body and the gonads are recalculated on the basis of strategies (1) to (3) for a ten year lifespan. The model fish is constrained to maintain its gonad condition and its gonadless body condition (GBC) ($=(W - W_g) \times 10^6/L^3$) between upper and lower limits. The gonad weight is not allowed to increase above 30% of the body weight or decrease below a minimum weight of 0.5 g and the GBC is constrained to stay between 10.0 and 3.35. The latter values were chosen after examination of the length and weight data of this study and Wilkins' (1967) data on starved Atlantic herring. The latter study reported that 50% mortality had occurred by the time the fish had reached a GBC of 3.35. Those fish were held in tanks and so predation was excluded, however, in the field predation would undoubtedly have increased that mortality rate. If the GBC of the model fish is greater than 10.0 then either length or gonad weight is increased, depending upon the strategy in use. If it is less than 3.35 then either growth in length is slowed or gonad weight is decreased depending upon the strategy being followed.

The fecundity at age for each strategy is shown in Fig. 19A and the cumulative fecundity at age in Fig. 20. Strategy (1) is found to convey the most fitness at all ages followed by strategies (3) and (2). This result will be

Fig. 19. A. The fecundity at age for strategies 1, 2 and 3 and the mean fecundity when rations are unaltered. The inset shows the values of δ calculated using a pseudo-random normal number generator with a mean of 0 and a standard deviation of 0.1.

B. The mean annual gonadless body condition index (GBC) of a herring following strategies 1, 2 and 3 and the mean GBC when rations are unaltered.

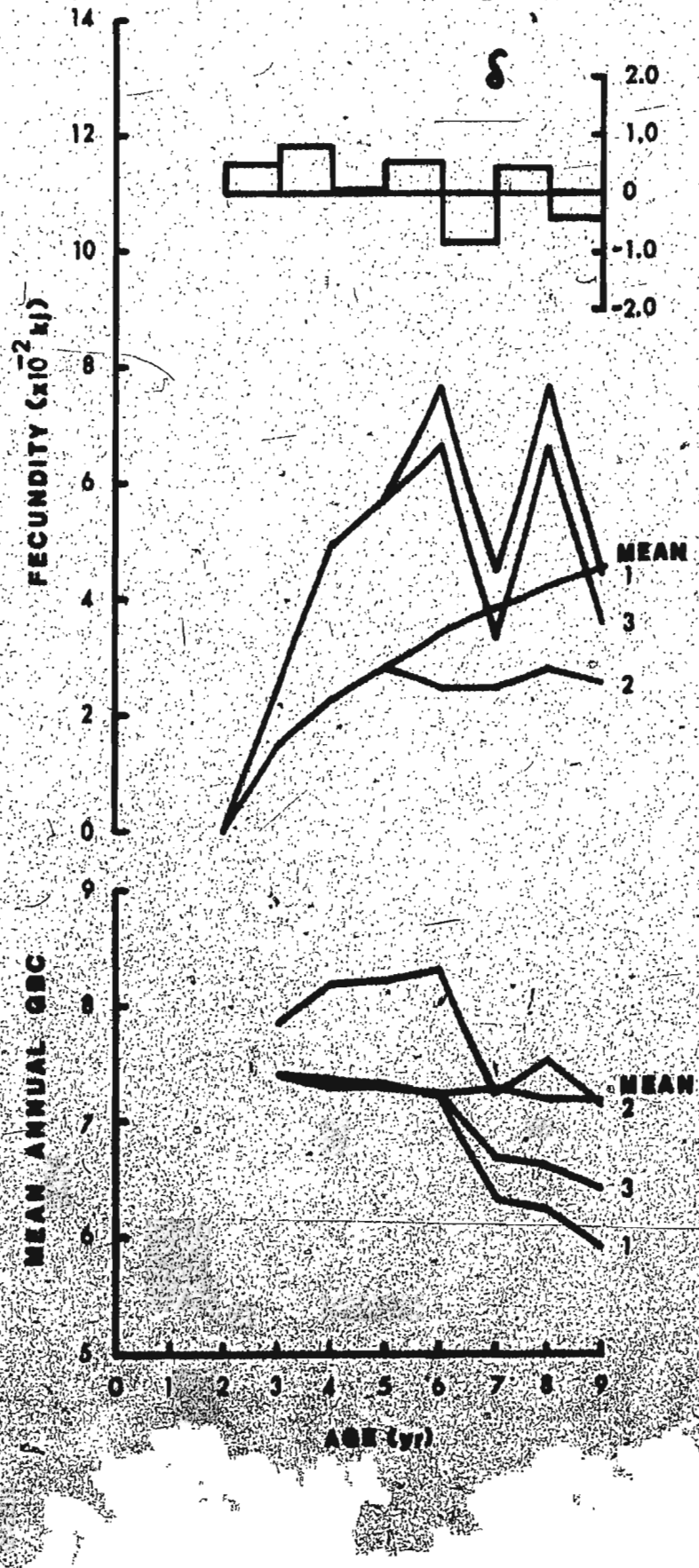
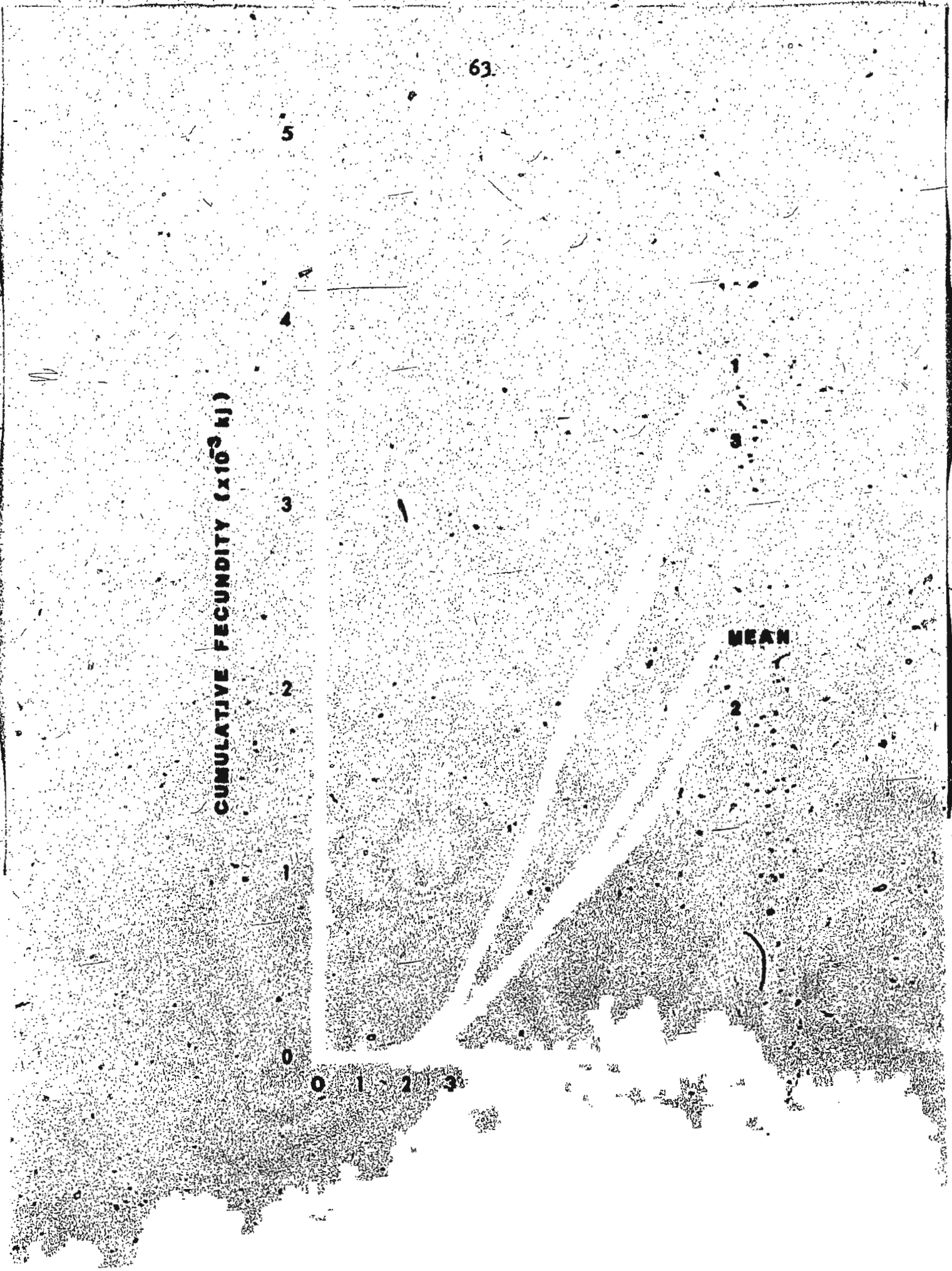

δ
2.0
1.0
0
-1.0
-2.0
FECUNDITY (x10⁻² kJ)
14
12
10
8
6
4
2
0
MEAN
1
3
2
MEAN ANNUAL GSC
9
8
7
6
5
MEAN
2
3
1
0 1 2 3 4 5 6 7 8 9
AGE (yr)

Fig. 20. The cumulative fecundity at age of strategies 1, 2 and 3 and the mean fecundity when the rations rate is unaltered.


CUMULATIVE FECUNDITY (x10^3 ml)
5
4
3
2
1
0
0
1
2
3
MEAN
1
3
2

found regardless of the values of δ because strategy (3) can only result in a fecundity equal to or less than that of strategy (1).

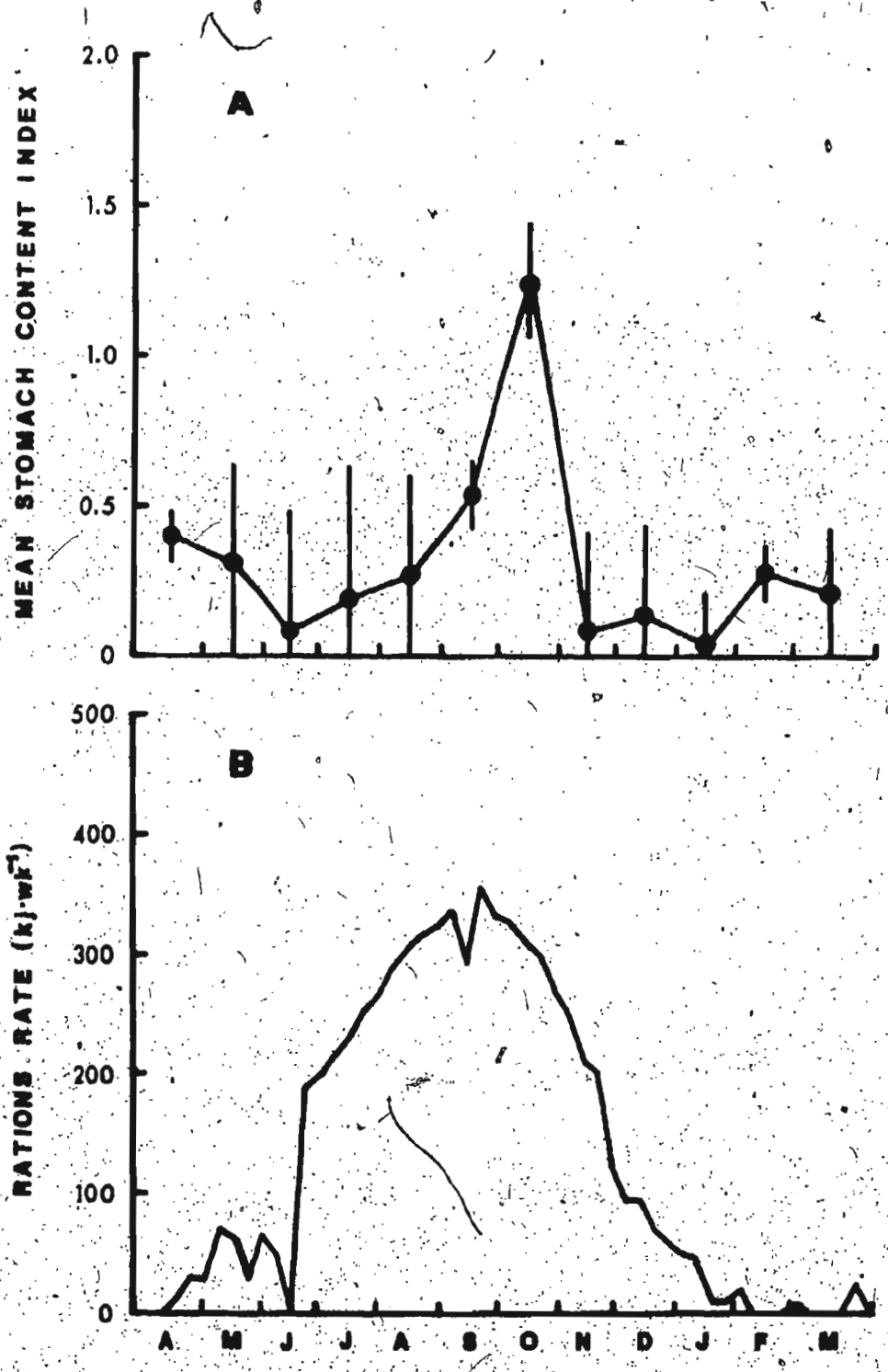
The question of which strategy is followed by the herring is still ambiguous because of the fact that increased fitness is accompanied by decreased mean GBC (Fig. 19B). This will offset the advantage in fitness by increasing the mortality rate of a fish following this strategy, i.e. there is a tradeoff between increased fecundity and increased mortality. It is difficult to examine this question quantitatively because we can only speculate on the nature of the relationship between GBC and the probability of mortality.

Discussion

The validity of the model can be determined by comparing the calculated energy flow rates with independent estimates of the same energy flow rates. Some workers (Daan 1973; Jones 1978) have obtained estimates of the food ingestion rate by using empirical data on stomach contents and on the gastric emptying rate. Stomach content frequency data is available for the herring of the stocks about the Avalon Peninsula for the years 1968-1976 (G. Winters, Biological Station, St. John's, Newfoundland) and from it was calculated a monthly mean stomach content index (SCI). It was calculated in the following way; each stomach was assigned a number on the basis of the volume of food it contained: a full stomach = 4; three-quarters full = 3; half-filled = 2; one-quarter filled = 1; empty = 0. The frequency of each category was then multiplied by its value and divided by the total sample size for each month (Fig. 21A). It must be noted that the SCI is not an index of the actual food ingestion rate since it has not been corrected by the gastric emptying rate which is a function of temperature and rations rate. There are, at present, no estimations of the manner in which the gastric emptying rate varies with temperature and rations rate for herring. Instead the SCI is a rough index of the feeding schedule of the herring. The SCI reaches a maximum in October and the modelled rations rate curve reaches a maximum in late September and early October (Fig. 21B).

The exponent of the fecundity-length relationship

Fig. 21. The seasonal distribution of two curves:
A, the mean monthly stomach content index of herring of the Placentia Bay-St. Mary's Bay-Conception Bay stock complex for the years 1968-1976. The bars are ± 1 s.d.
B, the modelled seasonal rations rate for a 4-5 year old herring.


A
MEAN STOMACH CONTENT INDEX
2.0
1.5
1.0
0.5
0
B
RATIONS RATE (kJ·wF⁻¹)
500
400
300
200
100
0
A M J J A S O N D J F M

is calculated as 4.35 (Fig. 15) which is very close to the value of 4.5 reported by Hodder (1972) for herring of Placentia Bay. If the age corrections of the body condition index and the ovary condition index are not utilized the exponent is only 2.3.

The ratio of annual total production to the annual rations rate (total P/R) (Fig. 16) declines with age. This appears to be a universal phenomenon; similar results have been reported by Lasker (1970) and Jones (1976) and predicted by Ware (1978). Its cause is the fact that total metabolic expenditure increases at a faster rate with age than rations rate thus steadily reducing the energy available for growth. The range of values of the total P/R curve is 0.064 - 0.141. This range can be compared with others reported in the literature. An estimate of the P/R ratio of juvenile herring was extracted from the study performed by DeSilva and Balbontin (1976). The reported gross conversion efficiencies were converted to energy units by assuming that the energy density of the food was 3.82 kj g^{-1} (see p. 46) and that the energy density of the herring tissue was equal to the mean energy density of the herring tissue of this study. The recalculated P/R ratios of fish weighing 7.8 - 18.8 g ranged from 0.173 at 14.5 C to 0.300 at 6.3 C. Jones (1976) reported a range of 0.15 to 0.45 for a number of fish species. Both of these two ranges are far above that predicted by the model. There are two possible reasons for the disparity: (i) Jones' values were calculated using

units of weight rather than units of energy and so his values can only be compared to the predicted values if the energy density of the food was identical to the energy density of the fish flesh, a situation that has often been assumed in energetics studies (Paloheimo and Dickie 1966) but rarely shown to be the case; and (ii) the time scales used in calculating the P/R ratios are different. The predicted ratios are calculated for an annual time period whereas the studies reported by Jones and DeSilva and Balbontin lasted a few months. The conversion efficiency calculated for a period of near satiation feeding is most likely quite different from the efficiency calculated for a time interval that includes periods of non-feeding as well as feeding. In fact it is most likely to be higher, a statement that it supported by Lasker's (1970) report of a calculated annual conversion efficiency of 0.06-0.15 for the Pacific sardine.

Ware (1978) presented theoretical reasons for assuming that $R_{annual} = gW^b$ where b = 0.7 - 0.8. Jones (1978) calculated b as 0.77 - 0.80 for haddock and 0.8 - 1.3 for cod. The value of the exponent calculated in this study (Fig. 17) is 0.66 which means that the rate of increase of

R_{annual} per unit body weight is less than that of cod and haddock. It does not mean that the annual rations rate per unit body weight is less than that of cod or haddock since that depends on the value of q, the proportionality constant. One possible reason for the relatively low exponent value is that the model deals only with herring of the length range 210.0 - 350.0 mm. The most rapid changes in the relationship between annual rations rate and body weight would be expected to occur in the smaller length classes and so their inclusion could possibly increase the exponent value.

This model is not an end in itself. Ideally it is a research tool with a number of possible applications. It could serve as a building block of a larger model of the pelagic ecosystem of the North Atlantic. One application of this larger model would be the testing of the hypothesis, originally proposed in regard to the Gulf of St. Lawrence herring stock complex (Winters 1976), that herring biomass is controlled by competition with mackerel for a limited pelagic food resource. The model could also serve to estimate pollutant uptake in herring. Another application would be the estimation of a time budget to be used as an adjunct to a study of herring behaviour. One application which did not require great amounts of additional data was an examination of the consequences of various strategies of energy allocation between the gonad and the soma. The conclusion of the exercise is that there is a tradeoff between the fecundity and the condition index. The exact form of the

relationship is unknown and so we are unable to state categorically which strategy is optimal for Atlantic herring. Even if this is possible it may not be meaningful since there may be many locally optimum strategies each appropriate for the particular combinations of mortality rate and food production cycle variability found in different oceanographic regions.

A related subject is the question of the ultimate cause of death in older fish. It has been speculated that it is the result, directly or indirectly, of the loss of body condition resulting from the geometric increase in the energy requirements of gonad growth with age (Hislop 1975; Ware 1975). On the other hand Cushing (1975) has supposed it to be the result of a process of senescence. Obviously the answer to this question depends on the strategy of energy allocation followed by a herring population. An older fish following strategy (1) will obviously have a higher probability of mortality than one following strategy (2).

Finally, it must be pointed out that more work must be done to derive more accurate descriptions of the physiological parameters of the Atlantic herring. Areas that require immediate attention include the scope of the metabolic rate, the estimation of α, the dependence of e_r on temperature and rations rate and the relative importance and numerical value of the transfer efficiencies between the gonads and the soma.

Summary

1. This study analyzes the seasonal energy flows within individual adult herring between 3-11+ years of age.
2. The seasonal cycle of the condition indices, the lipid and water content and the energy densities of the soma and the gonads were measured for a stock complex off the Avalon Peninsula, Newfoundland.
3. The testes grow at a faster rate than the ovaries during the summer, reach a maximum weight before overwintering and remain at this weight throughout the winter and spring. The ovaries grow continuously throughout the winter and reach a maximum weight immediately before spawning.
4. There is no significant difference between the mean body condition index of males and that of females except in late summer when the males have a higher mean value.
5. The condition index of the body and the ovary is greater in older fish then young fish at any time of the year. The testes condition index does not change with age.
6. There is no significant difference between the energy densities and the percentage of lipid and water of the soma of the males and those of the females at any time of the year.
7. The percent lipid of the soma of the combined sexes does not vary with the length of the fish.
8. The percent lipid and the percent water of the soma and the testes vary inversely with each other. The percent

lipid of the wet weight of the ovaries is 1.23 ± 0.33% regardless of the percent water.

9. The energy conversion factors of the lipid and solid of the soma were found to be identical to the values reported in the literature. The same energy conversion factors, if used to calculate the energy content of the testes and the ovaries, introduced a 4.42% and an 11.79% error, respectively.

10. The energy density of the soma and the gonads is highly correlated (r = 0.99) with the percent water of the tissue.

11. A model of the energy budget of the fish was constructed. It generated a pattern of seasonal rations rate which matched observed data on the seasonal pattern of stomach content frequency. The exponent of the modelled fecundity - length relationship (4.35) was found to be close to an observed value for the Placentia Bay stock. The range of gross growth efficiencies (0.064-0.141) was found to be lower than any ranges reported in the literature. The exponent (0.66) of the regression of the log of the total annual rations rate on the log of the mean weight was found to be at the lower end of the range predicted by Ware (1978) and reported by Jones (1978).

12. A sensitivity analysis of the model revealed that the model output is most sensitive to variation in the metabolic rate parameters and least sensitive to variation

in the data on the condition indices, the energy densities and the annual growth increments.

13. The model was used to examine the consequences of three strategies of energy allocation between the soma and the gonads. There is a tradeoff between the fecundity and the body condition index but the exact form of the relationship is unknown and so the optimal strategy cannot be identified.

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APPENDIX A

Sample number	Length (cm)	Weight (g)	Sex[1]	Age	Mat. stage	Gonad wt.(g)	Liver wt.(g)	Head wt.(g)	Back wt.(g)
1-002	33.4	327.0	1	-	4	60.8	-	-	-
1-003	31.5	273.0	2	-	4	32.3	-	-	-
1-004	33.6	388.0	1	-	4	79.6	-	-	-
1-006	35.5	367.8	2	-	4	25.6	-	-	-
1-007	35.5	390.0	2	-	4	50.0	-	-	-
1-008	34.4	345.5	1	-	4	74.7	-	-	-
1-010	38.0	399.9	2	-	4	43.8	-	-	-
1-011	33.8	311.5	2	-	4	28.0	-	-	-
1-012	33.5	330.0	1	-	4	54.0	-	-	-
1-013	32.0	288.0	1	-	4	44.6	-	-	-
1-014	35.3	402.0	1	-	4	79.4	-	-	-
1-015	34.0	322.5	1	-	4	59.1	-	-	-
1-016	34.5	352.0	2	-	4	45.8	-	-	-
1-017	35.0	375.0	2	-	4	36.1	-	-	-
1-018	35.0	384.7	2	-	4	49.5	-	-	-
1-019	36.2	437.7	2	-	4	82.2	-	-	-
1-020	33.7	333.2	2	-	4	42.4	-	-	-
1-021	33.7	308.4	2	-	4	29.0	-	-	-
1-022	35.3	356.0	2	-	4	62.1	-	-	-
1-023	33.9	354.5	1	-	4	58.9	-	-	-
1-026	32.4	287.4	1	-	4	45.2	-	-	-
1-027	36.5	385.7	2	-	4	45.0	-	-	-
1-028	31.4	274.0	1	-	4	41.1	-	-	-
1-029	32.7	285.0	1	-	4	46.1	-	-	-
1-030	34.5	361.0	2	-	4	59.7	-	-	-
1-031	32.2	264.2	1	-	4	40.7	-	-	-
1-032	32.0	258.6	2	-	4	29.4	-	-	-
1-033	33.5	330.7	2	-	4	50.6	-	-	-
1-034	29.3	219.2	1	-	4	27.9	-	-	-
1-035	31.5	250.0	2	-	4	21.5	-	-	-
1-036	32.6	300.0	2	-	3	17.5	-	-	-
1-037	34.0	369.1	1	-	4	77.5	-	-	-
1-038	33.5	358.0	1	-	4	71.3	-	-	-
1-039	33.2	317.8	2	-	4	31.5	-	-	-
1-041	34.5	339.2	2	-	4	32.4	-	-	-
1-042	33.5	320.0	2	-	4	40.2	-	-	-
1-043	33.0	343.3	1	-	4	56.5	-	-	-
1-044	35.5	406.0	1	-	4	82.5	-	-	-
1-045	33.6	348.5	2	-	4	46.6	-	-	-
2-001	35.5	436.3	2	11	4	83.7	-	-	-
2-004	35.7	374.5	2	11	4	49.3	-	-	-
2-005	33.7	356.0	1	9	4	69.0	-	-	-
2-006	32.2	307.2	1	8	4	-	-	-	-
2-007	33.8	330.0	2	9	4	57.9	-	-	-
2-008	35.4	393.4	2	11	4	62.0	-	-	-
2-009	34.2	353.8	2	7	4	54.7	-	-	-

[1] 1 = male; 2 = female

Sample number	Length (cm)	Weight (g)	Sex	Age	Mat. stage	Gonad wt. (g)	Liver wt. (g)	Head wt. (g)	Back wt. (g)
2-010	33.3	305.5	1	9	4	51.3	-	-	-
2-011	34.8	362.2	2	5	4	40.0	-	-	-
2-012	34.5	329.9	2	9	4	39.5	-	-	-
2-013	34.9	392.7	1	11	4	76.1	-	-	-
2-014	34.0	350.8	1	8	4	65.3	-	-	-
2-015	35.2	334.9	1	9	4	59.2	-	-	-
2-016	34.8	375.7	1	11	4	78.3	-	-	-
2-017	33.4	316.9	2	5	4	26.2	-	-	-
2-018	34.8	327.2	2	9	4	52.5	-	-	-
2-019	34.5	353.2	1	5	4	52.5	-	-	-
2-020	36.9	421.3	2	11	4	64.1	-	-	-
2-021	35.5	412.6	2	11	4	67.4	-	-	-
2-022	32.5	290.0	2	5	4	31.6	-	-	-
2-023	34.6	354.3	2	9	4	42.9	-	-	-
2-024	33.8	343.9	1	9	4	59.4	-	-	-
2-026	34.8	382.5	2	9	4	71.7	-	-	-
2-027	35.8	430.2	2	11	4	78.0	-	-	-
2-028	34.9	368.1	1	11	4	65.4	-	-	-
2-029	34.5	354.5	2	9	4	53.1	-	-	-
2-030	31.8	266.3	2	5	4	23.3	-	-	-
2-031	37.4	443.5	1	11	4	85.0	-	-	-
2-032	35.1	413.4	2	11	4	73.5	-	-	-
2-033	33.4	283.4	1	8	4	44.2	-	-	-
2-034	32.3	300.0	1	5	4	46.0	-	-	-
2-035	32.5	316.2	2	5	4	35.4	-	-	-
2.037	36.0	431.1	2	11	4	68.6	-	-	-
2-038	35.6	360.3	2	11	4	58.1	-	-	-
2-039	34.7	336.0	2	8	4	32.8	-	-	-
2-040	31.7	368.9	1	5	4	41.5	-	-	-
3-001	34.2	332.3	1	9	4	64.3	-	-	-
3-002	32.7	298.7	1	5	4	47.4	-	-	-
3-003	36.1	408.8	2	11	4	83.4	-	-	-
3-004	34.0	375.0	2	9	4	72.7	-	-	-
3-005	33.2	298.7	1	8	4	46.1	-	-	-
3-006	33.2	360.8	1	11	4	67.7	-	-	-
3-007	33.2	308.4	1	5	4	49.2	-	-	-
3-008	35.3	371.6	2	8	4	64.2	-	-	-
3-009	34.2	359.1	2	9	4	65.7	-	-	-
3-010	32.3	278.9	2	5	4	43.1	-	-	-
3-012	32.8	304.2	1	8	4	55.5	-	-	-
3-020	33.2	299.3	2	5	4	34.2	-	-	-
3-021	33.0	304.1	1	10	4	52.6	-	-	-
3-026	36.0	383.1	2	10	4	61.0	-	-	-
3-027	35.0	385.7	2	9	4	70.5	-	-	-
3-028	34.9	312.9	1	11	4	46.6	-	-	-
3-029	34.4	329.0	1	10	4	62.1	-	-	-
3-030	33.6	297.1	1	8	4	40.0	-	-	-

Sample number	Length (cm)	Weight (g)	Sex	Age	Mat. stage	Gonad wt.(g)	Liver wt.(g)	Head wt.(g)	Back wt.(g)
3-031	34.8	350.0	1	9	4	53.8	-	-	-
3-032	34.0	330.2	2	9	4	39.8	-	-	-
3-033	33.4	285.5	1	5	4	49.6	-	-	-
3-034	34.0	334.2	2	9	4	55.7	-	-	-
3-036	34.6	357.8	2	9	4	61.2	-	-	-
3-038	34.8	272.2	2	6	4	62.1	-	-	-
3-039	34.3	311.9	2	5	4	33.3	-	-	-
3-040	32.7	285.4	1	5	4	44.0	-	-	-
4-001	33.9	310.0	1	8	4	56.0	-	-	-
4-002	34.1	340.3	2	9	4	73.6	-	-	-
4-004	33.5	331.5	2	11	4	62.2	-	-	-
4-005	35.0	328.2	2	9	4	51.1	-	-	-
4-006	33.1	290.9	1	9	4	40.0	-	-	-
4-008	33.1	280.4	1	8	4	36.7	-	26.0	10.1
4-009	33.5	310.7	2	9	4	59.7	-	24.2	14.1
4-010	34.1	352.1	2	9	4	65.0	-	25.8	17.2
4-011	33.4	310.4	1	8	4	53.4	-	23.9	12.6
4-012	33.6	310.0	2	8	4	47.2	-	26.8	13.8
4-013	35.4	385.0	2	11	4	85.7	-	29.0	16.3
4-015	35.5	375.5	2	9	4	65.0	10.6	28.9	13.6
4-016	33.4	305.2	2	8	4	51.7	6.7	24.5	11.0
4-018	33.8	329.2	2	9	4	60.7	6.1	26.2	10.5
4-018	36.2	372.9	1	11	4	56.8	-	31.9	13.8
4-019	34.0	321.8	2	9	4	48.2	6.7	26.3	11.9
4-020	33.6	310.9	2	8	4	60.5	6.5	26.2	10.8
4-021	32.7	255.8	2	8	4	21.8	5.3	23.0	10.0
4-022	34.5	355.1	2	8	4	51.1	9.1	27.4	12.8
4-023	34.3	336.5	2	9	4	60.8	6.7	25.6	11.8
4-024	34.2	301.6	1	9	4	29.2	-	24.9	11.4
4-025	35.8	361.8	1	11	4	48.4	-	31.1	13.7
4-027	36.6	403.3	2	11	4	77.4	9.1	30.8	14.6
4-028	36.4	377.4	1	11	4	67.9	4.4	30.0	13.1
4-029	34.9	338.0	2	9	4	52.3	7.8	27.0	11.5
4-030	34.0	321.4	1	9	4	53.3	3.6	23.8	11.7
4-031	35.3	328.7	2	9	4	65.3	7.0	24.5	12.8
4-032	36.3	397.9	1	9	4	60.5	5.5	28.3	12.8
4-033	33.7	290.0	1	9	4	37.0	3.8	23.7	12.0
4-034	33.3	275.6	1	8	4	38.6	3.0	22.4	9.7
4-035	33.4	288.1	1	8	4	49.9	3.1	23.5	10.6
4-036	33.1	282.9	1	8	4	36.3	3.5	25.1	11.1
4-037	33.6	269.6	1	9	4	36.4	3.7	22.9	11.1
4-038	34.7	-	1	8	4	45.2	4.9	27.1	-
4-039	33.7	297.2	1	9	4	47.2	4.2	25.0	11.1
4-040	33.7	288.1	1	9	4	40.8	3.8	24.2	10.9
5-001	34.9	306.4	1	9	4	40.3	3.32	25.2	19.8

Sample number	Length (cm)	Weight (g)	Sex	Age	Mat. stage	Gonad wt. (g)	Liver wt. (g)	Head wt. (g)	Back wt. (g)
5-002	35.3	369.4	2	11	4	65.1	6.48	26.4	22.9
5-004	34.3	361.0	2	8	4	71.8	4.65	27.4	18.9
5-006	34.9	382.4	2	11	4	74.4	5.23	29.7	18.2
5-007	34.2	294.5	1	9	4	30.1	3.40	26.4	14.0
5-008	33.7	283.4	1	8	4	36.7	3.03	23.8	15.0
5-009	34.6	312.6	1	9	4	62.1	2.65	27.3	16.5
5-010	33.9	301.6	2	11	4	53.1	6.49	25.7	17.3
5-012	32.4	242.3	1	7	4	13.1	3.40	22.9	13.1
5-013	32.0	240.9	2	5	4	21.5	6.37	21.0	13.5
5-014	34.0	273.3	2	9	4	47.7	4.49	23.4	12.1
5-015	32.9	269.6	2	7	4	37.2	6.85	21.8	12.5
5-016	35.1	330.3	2	11	4	55.1	8.36	25.2	15.9
5-018	32.0	218.6	1	8	4	22.5	3.47	22.7	11.0
5-019	32.8	275.0	1	9	4	30.9	2.84	23.5	14.9
5-020	31.4	250.8	2	5	4	33.2	5.63	18.9	10.0
5-021	34.9	347.5	2	10	4	72.5	6.64	27.4	17.1
5-022	32.9	283.1	1	8	4	40.8	3.06	23.2	13.6
5-024	32.5	262.6	2	7	4	39.0	6.16	22.4	13.3
5-025	32.4	228.8	2	6	4	10.6	4.99	21.0	12.5
5-026	33.9	331.1	2	9	4	56.5	6.12	23.8	13.4
5-027	36.5	400.2	2	9	4	99.5	3.29	28.6	15.1
5-030	34.3	335.7	2	9	4	78.1	3.67	24.9	13.6
5-034	35.4	381.4	1	9	4	69.3	5.60	28.6	12.1
5-037	34.8	351.5	1	11	4	38.4	6.75	28.5	14.6
5-038	33.5	266.2	1	5	4	31.6	3.10	20.8	12.7
5-039	33.0	322.7	1	8	4	61.9	2.78	24.8	14.0
5-040	37.0	373.1	2	11	4	55.0	4.23	31.2	17.9
6-001	33.0	265.0	2	8	5	45.4	3.91	22.0	12.0
6-002	33.5	316.0	1	8	5	70.3	2.26	26.0	12.0
6-003	34.6	331.0	1	9	5	59.8	3.06	25.0	14.5
6-004	33.5	268.0	2	9	6	24.5	4.62	24.0	12.5
6-005	33.4	325.0	1	9	5	70.8	3.08	27.0	13.0
6-006	33.6	275.0	2	8	5	48.2	4.51	23.0	10.0
6-007	32.8	277	1	8	5	38.0	2.91	24	9
6-008	33.6	276	1	9	5	53.6	2.91	24	13
6-009	34.4	322	2	9	5	53.4	3.92	27	11
6-010	33.6	279	1	9	5	49.7	2.70	23	9
6-011	29.1	268	1	3	5	9.9	2.15	16	7
6-012	35.5	401	2	11	6	94.5	5.65	31	12
6-013	34.5	316	2	11	6	36.4	3.81	28	10
6-014	34.9	330	1	11	5	39.0	5.30	24	9
6-015	35.3	363	2	9	6	75.7	3.11	28	12
6-016	34.4	302	2	9	6	45.4	2.59	26	13
6-017	31.8	260	1	7	5	38.6	3.67	19	8
6-018	33.9	311	1	8	5	62.8	3.09	24	10
6-019	35.5	309	2	9	6	43.5	3.63	26	12

Sample number	Length (cm)	Weight (g)	Sex	Age	Mat. stage	Gonad wt.(g)	Liver wt.(g)	Head wt.(g)	Back wt.(g)
6-020	32.9	249	2	8	6	33.5	2.87	23	11
6-022	32.1	263	1	8	5	42.8	2.86	22	8
6-023	32.7	325	2	8	5	67.5	3.10	25	9
6-024	33.8	311	1	8	5	55.2	1.58	24	10
6-025	32.0	264	1	8	5	48.1	3.38	23	11
6-026	30.9	245	2	4	5	18.3	5.72	18	9
7-002	36.4	335.2	1	11	2	4.5	5.59	30.5	14.7
7-003	36.0	326.5	1	11	2	5.2	6.66	26.2	13.5
7-005	33.4	262.6	2	8	2	3.5	4.43	23.5	11.7
7-006	33.3	320.0	1	8	2	13.0	7.48	25.0	11.2
7-007	35.7	329.3	1	11	2	4.8	5.85	28.4	14.6
7-009	34.8	329.4	2	9	2	4.0	5.99	24.9	11.5
7-010	33.9	313.3	1	9	2	6.5	6.30	23.9	10.0
7.011	33.6	292.6	2	8	2	4.6	6.92	23.0	9.7
7-012	33.7	311.3	1	9	2	6.1	5.82	25.1	9.3
7-013	35.1	300.0	2	8	2	3.5	6.34	26.6	11.1
7-014	34.0	321.0	1	9	2	4.6	5.81	24.9	9.6
7-016	33.8	271.4	2	9	2	3.2	3.41	25.7	11.4
7-017	36.0	340.4	2	11	2	5.1	5.32	26.5	11.8
7-018	35.0	318.3	2	10	2	4.6	5.96	24.7	11.2
7-019	34.0	279.6	1	9	2	4.5	3.52	23.7	10.3
7-020	34.4	315.1	1	9	2	3.6	5.62	24.0	10.7
7-021	35.1	335.6	1	11	2	3.1	4.74	32.9	13.1
7-023	34.1	309.7	1	11	2	5.7	4.14	25.2	-
7-024	34.1	300.3	1	9	2	2.2	6.59	25.4	-
7-025	33.6	295.8	2	9	2	4.0	6.10	23.8	-
7-026	34.2	296.2	1	9	2	4.2	5.01	25.3	-
7-027	35.3	334.1	1	11	2	4.8	5.32	27.2	-
7-028	33.4	301.3	2	9	2	4.5	4.69	24.3	-
8-002	34.9	376.6	1	11	4	68.8	2.97	29.3	12.5
8-003	35.1	249.4	2	11	4	28.9	6.38	28.8	11.9
8-004	33.8	310.0	1	9	4	40.7	3.69	24.9	10.1
8-005	33.5	317.3	1	9	4	65.7	1.80	24.8	9.1
8-006	34.9	336.2	2	11	4	24.9	7.46	25.9	12.1
8-007	35.4	338.9	1	11	4	47.1	4.77	28.5	12.1
8-008	32.4	270.3	2	9	4	17.2	5.38	23.2	9.1
9-009	35.7	391.1	2	11	4	21.3	7.88	31.7	11.7
8-010	34.5	306.1	2	11	3	13.1	5.57	27.5	11.7
8-011	34.9	330.2	1	11	4	61.8	2.50	27.5	12.6
8-012	33.3	293.3	2	9	4	23.5	5.70	24.6	11.4
8-013	36.6	364.3	2	11	3	12.2	5.75	31.3	13.6
8-014	33.6	299.2	2	9	4	19.3	6.42	25.0	10.6
8-016	33.7	299.7	1	9	4	39.1	2.42	25.9	10.8
8-017	33.5	293.2	1	9	4	48.3	2.83	25.0	11.3
8-018	35.0	344.4	1	9	4	38.2	3.18	27.1	11.9
8-019	32.8	263.6	2	9	4	17.8	5.48	24.7	11.2
8-020	33.2	296.3	1	9	4	53.9	1.93	25.0	9.9

Sample number	Length (cm)	Weight (g)	Sex	Age	Mat. stage	Gonad Wt. (g)	Liver wt. (g)	Head wt. (g)	Back wt. (g)
8.021	33.4	317.1	1	9	4	53.7	1.89	24.4	9.4
8-022	33.9	326.1	1	9	4	57.9	3.06	22.9	10.4
8-023	33.3	309.6	2	9	3	17.5	6.71	26.3	10.1
8-024	33.9	313.5	1	9	4	56.3	1.96	24.6	9.8
8-025	33.6	284.8	2	9	3	15.0	5.41	25.2	11.9
8-026	34.0	305.0	1	9	4	49.6	2.29	26.2	11.4
8-027	33.4	328.8	1	9	4	57.8	2.52	29.3	10.7
8-028	34.3	305.1	2	9	4	20.4	6.83	26.0	11.5
8-029	34.5	317.9	2	9	3	19.4	6.71	27.5	10.7
8-030	34.5	288.6	2	11	3	15.8	4.49	27.5	11.0
8-031	33.9	278.5	2	9	3	13.9	4.86	24.5	9.9
8-032	33.2	312.5	1	9	4	47.5	3.01	23.9	10.6
8-033	35.7	379.1	1	11	4	64.0	2.29	30.6	-
8-034	34.0	325.3	1	9	4	40.6	2.40	24.4	-
8-035	34.2	298.1	2	9	3	17.2	6.60	26.4	-
8-036	33.9	280.8	2	9	3	15.6	6.37	24.9	-
8-037	33.8	324.5	2	9	4	25.5	5.77	28.4	-
8-038	32.0	284.6	1	8	4	56.2	1.57	23.9	-
8-039	32.7	283.6	1	8	4	46.9	2.14	25.1	-
8-040	33.4	299.8	2	10	3	18.1	6.17	25.4	-
8-041	32.7	311.4	1	8	4	58.0	2.18	23.6	-
8-042	34.7	313.6	2	10	3	18.2	4.45	29.1	-
8-043	34.5	323.2	1	9	4	56.5	2.25	27.3	-
8-044	35.9	324.1	2	11	4	27.6	6.27	30.7	-
8-045	33.8	285.0	2	9	3	18.8	4.48	25.8	-
8-046	33.9	292.8	2	9	3	13.0	5.78	26.3	-
8-047	34.5	312.2	2	9	3	14.2	6.04	26.6	-
9-001	33.9	315.5	1	9	4	29.3	7.26	25.3	15.9
9-002	35.7	383.7	2	9	4	44.6	13.50	31.4	21.1
9-003	35.0	308.5	1	9	4	50.6	2.98	28.5	16.3
9-004	36.2	392.2	1	11	4	82.0	3.48	31.8	19.5
9-005	36.3	350.2	2	11	4	21.7	7.57	30.5	16.3
9-006	33.9	341.3	1	11	4	57.5	3.19	29.3	15.2
9-007	36.1	416.3	1	11	4	78.2	3.27	30.2	19.0
9-008	34.4	368.4	1	9	4	66.1	3.03	28.0	16.4
9-009	35.1	359.6	2	11	4	29.3	9.26	29.2	15.3
9-010	32.3	260.9	1	5	4	30.0	2.34	22.5	12.0
9-011	35.1	345.4	2	11	4	44.8	7.32	30.3	12.1
9-012	35.0	360.5	1	9	4	67.2	3.69	26.4	12.2
9-013	35.5	351.5	1	11	4	63.0	2.76	28.2	12.2
9-014	35.0	335.2	2	11	4	33.4	7.08	26.7	12.4
9-015	35.6	401.9	1	9	4	75.7	3.31	31.3	15.5
9-016	34.8	374.9	1	5	4	69.4	2.55	25.6	15.1
9-017	36.5	393.4	2	11	4	18.3	8.12	32.2	17.0
9-018	35.7	381.2	2	11	4	36.3	10.53	29.4	16.0
9-019	35.6	420.9	1	11	4	88.5	3.32	30.4	13.3
9-020	37.7	506.5	1	11	4	87.9	5.74	37.0	15.0
9-021	35.3	385.9	2	11	4	33.0	10.29	30.0	15.0

Sample number	Length (cm)	Weight (g)	Sex	Age	Mat. stage	Gonad wt. (g)	Liver wt. (g)	Head wt. (g)	Back wt. (g)
9-022	34.8	355.5	2	11	4	35.5	8.39	27.0	11.8
9-023	35.4	372.6	2	11	4	57.5	6.48	29.7	13.9
9-024	35.5	372.0	2	11	4	46.5	8.49	26.8	14.7
10-001	36.0	390.1	2	11	4	62.0	7.68	31.4	11.6
10-002	33.6	314.6	2	6	4	54.7	4.72	22.9	9.9
10-003	35.7	378.2	1	6	4	77.4	2.77	25.4	12.2
10-004	34.2	313.9	2	5	4	27.8	6.34	24.2	11.0
10-005	37.6	466.9	2	11	4	78.8	7.33	31.9	12.8
10-006	35.4	381.1	2	6	4	63.2	4.16	26.1	10.4
10-007	31.2	242.9	1	4	4	29.3	2.29	18.2	7.9
10-008	32.1	258.5	1	4	4	26.7	2.38	19.7	8.0
10-009	35.1	360.9	2	6	4	29.7	9.49	28.5	10.9
10-010	30.7	241.8	1	4	4	35.5	1.87	18.6	7.3
10-011	36.3	400.6	1	11	4	81.7	3.25	31.2	11.0
10-012	32.6	246.9	2	4	4	13.4	5.43	20.7	7.9
10-013	36.3	463.2	1	11	4	108.4	3.27	31.3	11.6
10-014	35.6	397.5	1	11	4	70.0	3.71	30.4	10.9
10-015	30.5	224.5	1	4	4	19.0	2.05	17.0	7.8
10-016	36.8	411.2	2	11	4	58.6	7.46	29.2	11.1
10-017	36.8	399.1	2	11	4	56.7	8.01	29.3	11.6
10-018	32.6	288.3	2	4	4	36.3	5.05	20.6	7.8
10-019	34.4	345.3	1	11	4	62.4	2.69	27.5	9.8
10-020	36.0	378.9	2	11	4	51.7	10.18	30.0	11.6
10-021	35.1	356.9	2	6	4	33.7	6.06	25.7	10.6
10-022	32.9	317.8	1	6	4	66.3	2.91	23.1	8.7
10-023	31.3	247.6	1	4	4	38.9	1.89	18.8	6.7
10-024	30.9	261.7	1	4	4	49.0	1.71	19.2	7.7
11-001	33.0	277.2	2	5	4	21.1	5.69	22.2	10.0
11-002	36.1	393.8	2	11	4	59.4	8.95	28.1	14.1
11-003	35.3	322.5	2	10	4	43.8	8.12	25.6	12.0
11-004	32.1	259.4	1	4	4	29.3	2.35	19.8	10.0
11-005	35.5	340.0	1	10	4	55.4	3.47	29.0	13.0
11-006	35.1	394.0	1	10	4	65.0	3.84	29.0	12.2
11-007	34.5	322.7	1	10	4	60.0	2.37	23.8	12.0
11-008	34.7	290.0	2	5	4	37.5	4.70	25.0	12.0
11-009	33.9	328.6	2	10	4	48.3	6.50	26.0	9.9
11-010	37.5	423.8	2	11	4	72.2	8.97	31.9	14.3
11-011	33.6	309.2	1	6	4	52.9	2.41	22.6	10.6
11-012	33.2	267.5	2	5	4	34.3	3.49	20.3	9.7
11-013	34.1	307.2	1	10	4	51.8	3.71	24.3	11.0
11-014	30.6	228.2	1	4	4	43.7	1.93	16.4	7.2
11-015	34.8	348.5	2	10	4	44.6	6.88	27.6	11.3
11-016	36.1	358.9	2	11	4	41.2	7.83	28.2	11.6
11-017	33.3	264.1	1	6	4	42.6	-	22.3	10.3
11-018	31.6	216.9	2	4	4	13.5	3.58	18.4	9.1
11-019	33.9	322.1	2	7	4	33.2	8.44	27.3	10.0
11-020	36.2	260.9	1	10	4	63.2	2.44	28.3	14.2

Sample number	Length (cm)	Weight (g)	Sex	Age	Mat. stage	Gonad wt.(g)	Liver wt.(g)	Head wt.(g)	Back wt.(g)
11-021	34.6	313.6	2	10	4	44.0	6.68	24.9	10.2
11-022	36.1	382.7	1	11	4	68.3	3.11	34.7	14.0
11-023	33.6	271.7	1	10	4	39.3	2.50	24.4	10.8
11-024	33.7	279.5	1	5	4	45.0	1.89	22.1	9.9

APPENDIX B

sample number	% Lipid			% water		
	soma	testes	ovary	soma	testes	ovary
2-001	12.57	-	1.03	68.22	-	65.16
2-004	11.53	-	0.89	68.79	-	66.37
2-005	13.55	4.07	-	66.94	70.02	-
2-006	17.13	2.83	-	63.30	75.22	-
2.008	15.34	-	0.86	65.70	-	65.02
2-009	14.07	-	1.24	66.60	-	64.73
2-010	13.27	3.57	-	67.47	71.32	-
2-011	16.85	-	1.01	-	-	65.36
2-012	15.72	-	1.20	65.67	-	66.56
2-013	17.42	3.75	-	65.04	71.07	-
2-014	14.71	3.89	-	67.01	71.01	-
2-015	9.08	3.68	-	71.33	72.19	-
2-016	12.82	3.74	-	68.06	71.23	-
2-017	16.24	-	1.16	64.79	-	67.73
2-018	14.96	-	1.44	66.34	-	63.96
2-019	16.96	3.74	-	63.73	71.68	-
2-020	16.41	-	1.62	65.40	-	65.15
2-021	13.97	-	0.99	66.91	-	64.74
2-022	16.75	-	1.75	64.56	-	65.37
2-023	12.29	-	1.61	68.07	-	65.37
3-001	11.02	3.51	-	69.68	70.37	-
3.002	16.29	2.55	-	64.90	74.54	-
3-003	14.18	-	1.12	67.18	-	64.44
3-004	12.91	-	0.86	67.98	-	64.32
3-005	11.42	3.52	-	69.36	71.00	-
3-006	10.11	3.65	-	70.39	70.72	-
3-007	14.71	3.06	-	66.49	72.52	-
3-008	12.59	-	0.95	68.61	-	64.99
3-009	-	-	1.19	-	-	64.58
3-010	15.28	-	1.10	65.16	-	64.68
3-012	-	3.91	-	-	70.52	-
3-020	15.45	-	1.95	65.99	-	66.06
3-021	8.80	3.55	-	71.18	70.35	-
3-026	14.54	-	1.05	66.72	-	64.60
3-027	13,80	-	0.99	67.52	-	65.57
3-028	8.47	3.60	-	71.29	69.47	-
3-029	5.70	3.48	-	74.18	71.38	-
3-030	6.46	3.63	-	73.15	69.75	-
3-031	12.77	3.03	0	68.20	73.20	-
3-032	15.03	-	1.60	66.42	-	67.00
3-033	11.30	3.77	-	69.42	71.79	-
3-034	13.88	-	1.21	66.43	-	64.73
3-036	11.99	-	1.12	69.10	-	64.68
3-038	12.94	-	1.95	67.44	-	64.81
3-039	13.15	-	1.29	66.95	-	65.70

sample number	% Lipid			% water		
	soma	testes	ovary	soma	testes	ovary
3-040	11.61	2.92	-	69.18	71.78	-
4-001	-	-	-	71.71	71.47	-
4-002	-	-	-	68.54	-	65.47
4-004	-	-	-	71.69	-	66.25
4-005	-	-	-	69.19	-	66.37
4-006	-	-	-	68.41	71.66	-
4-008	-	-	-	71.45	72.23	-
4-009	-	-	-	70.67	-	65.47
4-010	-	-	-	70.14	-	65.56
4-011	-	-	-	68.90	72.60	-
4-012	-	-	-	71.01	-	66.36
4-013	-	-	-	71.12	-	65.64
4-018	-	-	-	69.07	71.92	-
4-024	-	-	-	69.53	76.28	-
4-025	-	-	-	70.85	71.65	-
5-001	8.95	2.55	-	70.48	71.79	-
5-002	8.37	-	-	72.02	-	65.59
5-004	9.75	-	1.11	70.34	-	65.67
5-006	11.26	-	0.97	68.96	-	64.11
5-007	5.21	2.70	-	73.87	70.86	-
5-008	3.84	3.02	-	75.41	70.50	-
5-009	6.37	2.97	-	72.84	71.01	-
5-010	4.16	-	0.81	75.60	-	65.78
5-012	5.20	2.82	-	74.06	71.67	-
5-013	9.76	-	1.07	69.25	-	65.62
5-014	7.09	-	1.52	72.38	-	64.94
5-015	5.39	-	1.08	74.03	-	67.42
5-016	9.86	-	0.77	70.46	-	65.35
5-018	4.41	2.92	-	75.16	70.87	-
5-019	8.60	2.53	-	71.74	71.64	-
5-020	10.60	-	0.52	69.42	-	65.51
5-021	6.75	-	0.73	73.52	-	65.52
5-022	3.61	-	-	75.46	75.85	-
5-024	5.51	-	1.01	73.65	-	65.26
5-025	-	-	-	70.91	-	-
5-026	7.33	-	-	72.40	-	65.01
5-027	6.56	-	1.53	72.69	-	71.76
5-030	-	-	1.41	75.51	-	69.48
5-034	9.99	-	-	70.06	69.91	-
5-037	-	-	-	70.64	70.55	-
5-038	-	-	-	70.91	70.17	-
5-039	-	-	-	71.74	68.92	-
5-040	8.30	-	-	71.58	-	67.97
6-001	6.28	-	1.59	73.55	-	65.99
6-002	3.24	2.2	-	75.83	79.83	-

Sample number	% Lipid			% water		
	soma	testes	ovary	soma	testes	ovary
6-003	6.58	2.10	-	73.17	79.98	-
6-004	8.34	-	1.35	70.91	-	76.02
6-005	4.52	2.28	-	74.56	79.38	-
6-006	4.70	-	1.36	75.00	-	67.57
6-007	5.84	2.51	-	73.34	78.82	-
6-008	2.36	2.36	-	76.85	79.26	-
6-009	4.33	-	2.05	75.03	-	72.28
6-010	0.31	2.02	-	78.00	81.29	-
6-011	7.48	-	-	71.65	-	-
6-012	4.72	-	1.17	74.28	-	73.56
6-013	4.29	-	1.43	74.10	-	74.30
6-014	7.19	2.22	-	72.00	78.33	-
6-015	7.33	-	1.69	72.05	-	74.67
6-016	4.55	-	1.14	75.41	-	74.92
6-017	3.70	2.71	-	75.78	75.78	-
6-018	7.19	2.59	-	73.02	78.10	-
6-019	6.46	-	1.07	73.77	-	74.37
6-020	7.85	-	1.28	72.43	-	74.02
6-021	10.94	-	-	69.00	-	-
6-022	2.03	2.68	-	77.16	77.09	-
6-023	9.03	-	1.81	71.18	-	68.92
6-024	-	-	-	71.30	78.20	-
6-025	-	-	-	77.00	81.20	-
6-026	-	-	-	71.30	-	66.60
7-002	16.58	-	-	63.47	-	-
7-003	18.08	-	-	62.56	-	-
7-005	19.66	-	-	60.62	-	-
7-006	18.95	-	-	61.80	-	-
7-007	18.97	-	-	61.56	-	-
7-009	16.15	-	-	64.47	-	-
7-010	17.84	-	-	62.50	-	-
7-011	16.36	-	-	63.50	-	-
7-012	17.80	-	-	63.11	-	-
7-013	11.07	-	-	68.25	-	-
7-014	18.59	-	-	62.02	-	-
7-016	11.89	-	-	67.84	-	-
7-017	17.30	-	-	63.16	-	-
7-018	17.46	-	-	63.13	-	-
7-019	12.19	-	-	67.88	-	-
7-020	14.49	-	-	65.59	-	-
7-021	17.92	-	-	63.11	-	-
8-003	18.04	-	1.18	63.14	-	66.45
8-006	18.14	-	1.09	63.15	-	67.84
8-007	13.20	1.66	-	67.84	76.72	-
8-008	16.68	-	1.72	64.76	-	68.78
8-009	17.16	-	1.43	63.82	-	67.25

Sample number	% Lipid			% water		
	soma	testes	ovary	soma	testes	ovary
8-010	13.04	-	-	67.89	-	-
8-011	-	2.18	-	-	75.42	-
8-012	14.62	-	-	65.92	-	-
8-013	17.00	-	-	63.64	-	-
8-014	14.59	-	-	66.02	-	-
8-016	13.74	1.42	-	67.60	76.01	-
8-017	14.93	2.12	-	65.87	75.03	-
8-018	16.89	1.86	-	64.04	75.59	-
8-019	14.85	-	-	65.93	-	-
8-020	12.34	-	-	68.89	-	-
8-021	15.70	2.15	-	65.10	75.36	-
8-022	17.04	1.91	-	64.73	75.74	-
8-924	16.90	2.21	-	64.51	75.19	-
8-025	16.38	-	-	64.23	-	-
8-026	11.93	2.07	-	68.52	75.63	-
8-027	15.53	2.02	-	65.48	75.30	-
8.029	-	-	1.58	-	-	67.89
8-030	-	-	1.65	-	-	71.22
8-031	-	-	1.35	-	-	69.77
8-036	-	-	1.22	-	-	69.38
8-044	-	-	0.90	-	-	68.38
8-047	-	-	0.74	-	-	72.26
9-001	15.90	-	1.30	63.47	-	65.68
9-002	15.19	-	1.35	64.65	-	65.87
9-003	14.10	2.42	-	65.03	71.80	-
9-004	14.25	2.41	-	65.20	73.25	-
9-005	14.65	-	1.41	64.49	-	66.27
9-006	15.97	2.65	-	65.38	72.59	-
9-007	16.15	2.79	-	63.91	70.41	-
9-008	16.43	2.95	-	63.52	70.46	-
9-009	12.88	-	1.41	67.69	-	65.65
9-010	15.88	2.05	-	62.33	74.20	-
9-011	12.37	-	0.93	71.52	-	64.17
9-012	10.15	3.10	-	70.11	73.01	-
9-013	14.23	2.41	-	65.68	72.49	-
9-014	17.65	-	1.17	62.38	-	65.28
9-015	15.73	2.15	-	64.78	72.27	-
9-016	14.34	2.65	-	65.68	70.74	-
9-017	16.37	-	1.28	64.99	-	70.55
9-018	12.98	-	1.36	66.68	-	64.80
9-019	16.74	-	-	64.33	-	-
9-021	17.05	-	1.50	64.17	-	64.48
9-022	13.25	-	1.13	67.17	-	66.98
11-001	13.43	-	1.85	66.66	-	65.61
11-002	-	-	1.09	-	-	63.43

Sample number	% Lipid			% Water		
	soma	testes	ovary	soma	testes	ovary
11-003	14.77	-	0.65	65.35	-	63.42
11-004	15.86	1.71	-	-	74.33	-
11-005	11.14	1.88	-	68.74	73.53	-
11-006	12.76	3.76	-	68.21	69.88	-
11-007	11.40	3.45	-	67.94	69.62	-
11-008	13.36	-	0.63	65.69	-	63.13
11-009	14.63	-	0.94	65.73	-	63.91
11-010	17.22	-	1.11	63.34	-	63.64
11-011	12.26	3.00	-	67.23	70.36	-
11-012	15.66	-	0.88	63.49	-	63.66
11-013	14.31	3.45	-	65.73	68.36	-
11-014	16.34	1.63	-	64.06	74.51	-
11-015	16.85	-	0.76	62.48	-	63.85
11-016	8.87	-	-	69.53	-	-
11-017	14.74	-	-	65.16	-	-
11-018	13.45	-	-	65.47	-	-
11-019	17.71	-	1.39	63.37	-	66.15
11-020	11.18	-	-	68.61	-	-
11-022	12.22	3.84	-	67.42	68.96	-

Head

Sample number	% lipid	% water
7-027	9.07	69.23
7-028	9.07	69.23
11-008	11.37	67.99
11-009	11.31	68.98
11-010	11.53	68.80

APPENDIX C

Sample number	Energy Density (kilojoules/g wet wt.) soma	testes	ovary	head
3-002	10.474	5.499	-	-
3-003	9.444	-	8.802	-
3-004	9.063	-	-	-
3-005	8.491	6.415	-	-
3-008	8.968	-	8.667	-
3-010	10.016	-	-	-
3-012	-	6.217	-	-
3-028	-	6.718	-	-
3-031	8.966	5.835	-	-
3-032	9.787	-	8.091	-
3-034	9.584	-	8.685	-
3-039	9.270	-	8.414	-
3-040	8.608	6.215	-	-
4-001	7.258	6.329	-	-
4-002	8.754	-	8.553	-
4-004	7.423	-	8.317	-
4-005	8.459	-	8.321	-
4-006	8.653	-	-	-
4-008	7.495	6.253	-	-
4-009	7.984	-	-	-
4-010	8.035	-	8.559	-
4-011	8.647	6.084	-	-
4-012	7.735	-	8.340	-
4-013	7.688	-	8.512	-
4-018	8.340	6.232	-	-
4-024	8.194	5.207	-	-
4-025	7.924	6.306	-	-
5-001	7.973	6.312	-	-
5-002	7.497	-	8.511	-
5-004	8.125	-	8.502	-
5-006	8.725	-	8.981	-
5-007	6.574	6.498	-	-
5-008	6.934	6.578	-	-
5-009	7.038	6.445	-	-
5-010	5.918	-	8.350	-
5-012	6.477	6.243	-	-
5-013	8.483	-	-	-
5-014	7.253	-	8.702	-
5-015	-	-	7.903	-
5-016	8.164	-	8.638	-
5-018	6.034	6.484	-	-
5-020	8.415	-	8.506	-
5-021	6.920	-	8.481	-
5-024	6.720	-	-	-

Sample number	Energy Density (kilojoules/g wet wt.) soma	testes	ovary	head
5-037	7.884	6.592	-	-
5-038	7.735	6.625	-	-
5-039	7.500	6.891	-	-
6-001	-	-	8.240	-
6-002	5.751	4.383	-	-
6-003	6.956	4.358	-	-
6-004	7.712	-	5.777	-
6-005	6.310	4.472	-	-
6-006	6.097	-	7.868	-
6-007	6.743	4.622	-	-
6-008	5.328	4.457	-	-
6-009	6.065	-	6.753	-
6-010	4.745	4.078	-	-
6-011	7.323	-	-	-
6-012	6.357	-	6.484	-
6-013	6.290	-	6.193	-
6-014	7.269	4.745	-	-
6-015	7.262	-	6.201	-
6-016	6.040	-	6.092	-
6-017	5.842	5.326	-	-
6-018	7.079	4.742	-	-
6-019	6.631	-	6.201	-
6-020	7.198	-	6.289	-
6-021	7.066	-	-	-
6-023	7.761	-	7.591	-
6-026	7.783	-	-	-
7-002	10.707	-	-	-
7-003	11.214	-	-	-
7-005	11.685	-	-	-
7-006	11.376	-	-	-
7-007	11.112	-	-	-
7-009	10.253	-	-	-
7-010	10.942	-	-	-
7-011	10.373	-	-	-
7-012	10.772	-	-	-
7-013	8.564	-	-	-
7-014	10.772	-	-	-
7-016	8.709	-	-	-
7-017	10.662	-	-	-
7-018	10.710	-	-	-
7-019	8.680	-	-	-
7-020	9.635	-	-	-
7-021	10.757	-	-	-
7-024	-	-	-	6.735
7-025	-	-	-	6.802
7-026	-	-	-	6.735

Sample number	Energy Density (kilojoules/g wet wt.) soma	testes	ovary	head
8-003	11.013	-	8.016	-
8-006	11.119	-	7.687	-
8-007	9.234	5.012	-	-
8-008	10.399	-	7.398	-
8-009	10.839	-	7.889	-
8-010	9.155	-	-	-
8-011	-	5.314	-	-
8-012	9.892	-	-	-
8-013	10.763	-	-	-
8-014	9.843	-	-	-
8-016	9.325	5.109	-	-
8-017	9.930	5.377	-	-
8-018	10.705	5.276	-	-
8-019	9.949	-	-	-
8-020	8.840	-	-	-
8-021	10.197	5.340	-	-
8-022	10.521	5.285	-	-
8-024	10.593	5.371	-	-
8-025	10.565	-	-	-
8-026	8.835	5.281	-	-
8-027	10.130	5.329	-	-
9-001	-	-	8.443	-
9-002	10.430	-	-	-
9-004	10.122	-	-	-
9-005	10.325	-	8.286	-
9-006	10.328	6.090	-	-
9-007	10.663	6.557	-	-
9-008	10.854	-	-	-
9-009	9.224	-	8.466	-
9-010	10.961	5.642	-	-
9-011	8.355	8.901	-	-
9-012	8.196	5.966	-	-
9-013	9.953	6.039	-	-
9-014	11.288	-	8.439	-
9-015	10.179	6.016	-	-
9-016	9.935	6.410	-	-
9-017	10.478	-	6.874	-
9-018	9.508	-	8.673	-
9-021	10.717	-	8.765	-
9-022	9.307	-	7.984	-